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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 119, No. 1

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# REVISION OF FIVE AFRICAN SNAKE GENERA

By Arthur Loveridge

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
July, 1958

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# REVISION OF FIVE AFRICAN SNAKE GENERA

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July, 1958

No. 1 — *Revision of Five African Snake Genera*

By Arthur Loveridge

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## INTRODUCTION AND ACKNOWLEDGMENTS

This paper represents the author's last attempt at revising snake genera. The five dealt with here were selected because of the confused status of their component species, and this required elucidating in connection with the report on Nyasaland reptiles. The work was undertaken about 1950. The typescript was then laid aside with the intention of borrowing certain snakes on which questionable records were based, also in the faint hope of completing the African COLUBRIDAE, to which family these five genera belong. Eleven other colubrid genera have been dealt with already in three contributions to this Bulletin published in 1939, 1940 and 1944.

The procedure and format of the current contribution is essentially that of its predecessors, i.e. an attempt to synopsize all pertinent information appertaining to every species assigned to the genera under review. In the present instance the period covered is from 1880 to 1956, though the last year is possibly incomplete.

However, in the case of *Lycodonomorphus* Fitzinger, with which I synonymize *Glypholycus* Günther, I have treated the

little-known[1] *bicolor* of Lake Tanganyika in greater detail than usual. This is due to the collaboration of C. J. P. Ionides, Esq., who generously procured more than 100 specimens of this aquatic reptile for study. The astonishing variation displayed by this fine series is published here for the first time. One might add that Mr. Ionides also submitted comparably large quantities of at least one species for each of the four remaining genera.

Others in Africa who have aided this investigation by sending in material recently, are Messrs. D. C. Broadley (Southern Rhodesia), D. Vesey-FitzGerald (Northern Rhodesia), M. C. Lesage (Ghana) and J. S. Owen (Sudan).

During, and subsequent to, 1950 my esteemed colleague Dr. R. F. Laurent of the Musée Royal du Congo Belge has added several interesting species to the genera *Lycodonomorphus* and *Prosymna*. With the latter genus, Laurent's extensive West African material enabled him to clarify the situation respecting the races of *ambigua* occurring in the Belgian Congo. Though time and the accumulation of more material may demonstrate that two of these forms are untenable, I have accepted his arrangement except in one instance. Fortunately for me Laurent's researches prevented my merging *a. bocagii* with *a. ambigua*, something I was preparing to do because of the confusing misidentifications of *bocagii* in the literature, as may be seen from its synonymy. In acknowledgement of this, and as a tribute to Laurent's contributions to African herpetology, I take pleasure in naming the only novelty described in this paper:

PROSYMNA MELEAGRIS LAURENTI subsp. nov.

Circumstances have made it quite impossible for me to borrow paratypes of Laurent's new forms as I should have done if not so pressed for time. In other respects I have endeavoured to bring these revisions up to date as of 1956. At the time (*ca.* 1950) I first did them I borrowed much material or pestered herpetological correspondents for information respecting specimens in their care. For either one or the other I am indebted to the undermentioned colleagues and gladly avail myself of this opportunity of expressing my thanks.

[1] This was written before seeing Laurent's 1956 paper listing 133 specimens!

J. R. Bailey (Duke University); J. C. Battersby (British Museum); C. M. Bogert (American Museum of Natural History); G. S. Cansdale (Lyndale Avenue, London); B. S. Chauhan (Zoological Survey of India); D. M. Cochran (United States National Museum); R. Conant (Zoological Society of Philadelphia); J. Eiselt (Naturhistorische Museum, Vienna); V. F. FitzSimons (Transvaal Museum); J. Guibé (Paris Museum); N. Hartweg (Michigan University Museum); A. Holm (Zoological Museum, Uppsala); R. F. Laurent (Musée du Congo Belge); R. Mertens (Senckenberg Museum); M. G. Netting (Carnegie Museum, Pittsburgh); H. W. Parker (British Museum); J. A. Peters (Brown University, Providence); C. R. S. Pitman (Chelsea, London); M. Poll (Musée du Congo Belge, Tervueren); C. H. Pope (when at Chicago Nat. Hist. Mus.); H. Rendahl (Naturhistoriska Riksmuseet); W. Rose (South African Museum, Capetown); K. P. Schmidt (Chicago Natural History Museum); B. Shreve (Museum of Comparative Zoology); R. H. Smithers (National Museum, Bulawayo); O. van Straelen (Institut Royal de Belgique); P. E. Vanzolini (Departmento de Zoologia, São Paulo); H. Wermuth (Zoologisches Museum, Berlin); O. Wettstein (Osterreichische Akademie, Vienna); E. E. Williams (Museum of Comparative Zoology); G. F. de Witte (Institut Royal de Belgique).

When necessity arose to refer to this borrowed, or other, material, the institution where it may be found is indicated by the following abbreviations:

A.M.N.H., American Museum of Natural History, New York; B.M., British Museum (Natural History), London; C.M., Carnegie Museum, Pittsburgh; C.N.H.M., Chicago Natural History Museum, Chicago; I, Ionides field number; I.R.B., Institut Royal de Belgique; M.C.Z., Museum of Comparative Zoology, Cambridge; P.M., Museum National d'Histoire naturelle, Paris; R.G.M.C., Musée Royal du Congo Belge, Tervueren; S.M.F., Senckenbergische Naturforschende Gesellschaft, Frankfurt, a.M.; S.R.M., Southern Rhodesia Museum, Bulawayo; T.M., Transvaal Museum, Pretoria; U.S.N.M., United States National Museum, Washington.

*Localities.* An asterisk (*) *in front of* a place name implies that a specimen or specimens from said locality is either in the collection of the Museum of Comparative Zoology or has been

examined for this revision — as in the case of types studied at the British Museum in 1951. For one species only (*Lycodonomorphus r. rufulus*) the asterisk is *placed after* the locality to indicate that the material from these places is in the Transvaal Museum and was examined for me by Dr. V. F. FitzSimons with his customary kindness.

*Bibliography.* Owing to the spate of semi-popular books on snakes that have appeared in recent years, it is becoming increasingly difficult to know what should, or should not, be included. Where a date is followed by a letter of the alphabet it indicates that during the year cited the author in question published more than one paper on African herpetology. The letter has chronological significance in a more comprehensive bibliography of African Herpetology (1880-1953) which it is hoped may be published in the not too-distant future.

## Family COLUBRIDAE

### Genus LYCODONOMORPHUS Fitzinger

1843. *Lycodonomorphus* Fitzinger, Syst. Rept., p. 27. Type by original designation: *Coronella rufula* Schlegel = *Coluber rufulus* Lichtenstein.

1848. *Lycodontomorphus* Agassiz, Nomen. Zool. Index Universalis, p. 628. Emend. for *Lycodonomorphus* Fitzinger.

1863. *Xenusterophis* Günther, Proc. Zool. Soc. London, p. 16, footnote. Type by monotypy: *Natrix laevissima* Günther.

1893b. *Ablabophis* Boulenger, Cat. Snakes Brit. Mus., **1**, p. 318. Type by monotypy: *Coluber rufulus* Lichtenstein.

1894b. *Glypholycus* Günther, Proc. Zool. Soc. London, p. 629. Type by monotypy: *G. bicolor* Günther.

1924b. *Nerophidion* Werner, Sitzb. Akad. Wiss. Wien, **133**, Abt. 1, p. 53. Type by monotypy: *N. hypsirhinoides* Werner = *Glypholycus bicolor* Günther.

*Definition.* Maxillary teeth 18-25,[2] small, subequal; mandibular teeth longest anteriorly. Head slightly distinct from neck; eye

[2] In giving 18-19 for *bicolor*, possibly Cott (1935, p. 965) failed to allow for a missing tooth; there are clearly 19 in a ♀ skull (M.C.Z. 54091) and appear to have been 20 in another (M.C.Z. 30076). Günther said "about 21" for the type, while Boulenger (1896d, p. 615) merely stated that the dentition of *Glypholycus* was similar to that of *Lamprophis* and *Bothrolycus*. However, Laurent (1954b, p. 43) gives 19-20 teeth for both his *s. subtaeniatus* and *s. upembae*.

moderate, with round or vertically subelliptic pupil; nostril directed upwards, in a semi-divided or divided nasal; a loreal; preoculars 1, rarely 2; lateral head shields separated by an inconspicuous groove from the upper labials. Body cylindrical; scales smooth, with or without apical pits, in 19-25 rows; ventrals rounded; anal entire, rarely divided. Tail moderate, tapering; subcaudals paired.

Hemipenis of male not (*bicolor* and *subtaeniatus*) or distally bifurcate (*rufulus*); sulcus spermaticus forked. Hypapophyses present posteriorly in the vertebral column.

*Range.* African lakes and rivers south of 3° S.

*Remarks.* For earlier comments on the status of this genus and the number of pterygoid teeth, see Loveridge (1953e, p. 253) and Laurent (1954b, pp. 38-43). As Laurent's admirably described species and its race bridge the gap between *bicolor* and *laevissimus* in the west, as do *r. mlanjensis* and *r. whytii* between *bicolor* and *rufulus* in the east, there no longer remains any valid reason for retaining *Glypholycus* as a distinct genus. Bogert, on whose work (1940, pp. 18-19) I have depended in respect to dentition, hemipeneal and hypapophyseal characters, concurs in this view.

It is true that in *bicolor* the 4th labial is the only one to *normally* enter the orbit, whereas in all the other species both 4th and 5th are normal, and the 4th only is very exceptional. Such a character, however, cannot be considered of generic significance.

### *Key to the Species*

Our knowledge of the full range of ventral and subcaudal counts is so incomplete for certain forms, while in others the known counts display so much overlapping, that it appears next to impossible to devise a key that reflects relationships. However, if ranges are taken into account, and the table of statistical data that follows the key is consulted, the identification of specimens should be greatly simplified.

1. Midbody scale-rows 23, rarely 25 (25 present in only 2 of the 110 snakes examined); range: only Lake Tanganyika ..... *bicolor* (p. 9)
   Midbody scale-rows 21 to 23 (21 chiefly in ♂♂, 23 in ♀♀); range: western Angola and western Belgian Congo ..... 2
   Midbody scale-rows 19 to 21; range: eastern Belgian Congo and southern Nyasaland ..... 3

Midbody scale-rows 19, rarely 21 (21 present in only 2 of about 20 records of *laevissimus*); range: southern Tanganyika Territory; northern Nyasaland and Africa south of the Zambezi ..... 4

2. Subcaudals 29-40 (♀♀ 29-34; ♂ 40); ventrals 172-188 (♂ 172; ♀♀ 175-188); range: southeastern Belgian Congo ... *s. upembae* (p. 12)
Subcaudals 41-58 (♀♀ 41-48; ♂♂ 52-58); ventrals 175-193 (♂♂ 175-180; ♀♀ 189-193); range: western Belgian Congo and western Angola ... *s. subtaeniatus* (p. 13)

3. Throat of adult whitish to gray; belly mostly black sparsely flecked with cream; tail below entirely, or almost entirely, black (a young one under 230 mm. in total length, pure white; juveniles from 250-600 mm. gradually assume adult coloring, that is of 600-800 mm. specimens); range: montane streams of eastern Belgian Congo from north end of Lake Tanganyika to region of Lake Upemba ..... *r. leleupi* (p. 14)
Throat of adult to anus immaculate white; tail from anus to near its tip white with a dusky median line; range: montane streams of Zomba, Mlanje and Cholo Mountains, southern Nyasaland ..... *r. mlanjensis* (p. 16)

4. Subcaudals less than 50 (but that of ♂♂ unknown); range: southern Tanganyika Territory (where they approach *leleupi* in color) to northern Nyasaland; possibly also Charre, Mozambique ..... *r. whytii* (p. 17)
Subcaudals more than 50 (54 to 81; those reported as having less than 54, which I have examined, all had regenerated tail tips); range: south of the Zambezi ..... 5

5. Loreal well separated from first labial; ventrals 160 to 178; subcaudals 54 to 78; pupil subcircular, rarely round; no light line from behind eye to above corner of mouth; upper labials immaculate; underside immaculate or, at most and that but rarely, a few dusky marks; range: streams of Southern Rhodesia and Bechuanaland, south to Natal, west to the Cape ..... *r. rufulus* (p. 19)
Loreal in contact with first labial or, if separated, only by a granule; ventrals 172 to 183; subcaudals 58 to 81; pupil round; a more or less light line from behind eye to above corner of mouth; upper labials spotted; underside from throat to end of tail with a dusky median line or occasionally a median series of dusky markings; range: Transvaal (1 record), south to Natal (1 record), east through Cape Province ..... *laevissimus* (p. 23)

## STATISTICAL DATA FOR THE SPECIES OF LYCODONOMORPHUS

(Abnormal variations are given in parentheses)

| Species | Midbody scale-rows | Male ventrals | Female ventrals | Female subcaudals | Male subcaudals |
|---|---|---|---|---|---|
| *bicolor* | 23(-25) | 154-164 | 152-166 | 52-59[3] | 63-71[4] |
| *s. upembae* | 21-23 | 172 | 175-188 | 29-34 | 40 |
| *s. subtaeniatus* | 21-23 | 175-180 | 189-193 | 41-48 | 52-58 |
| *r. leleupi* | 19-21 | 165-171 | 164-174 | 52-61 | 65-67 |
| *r. mlanjensis* | 21 | 163-167 | 169 | 51 | 60-71 |
| *r. whytii* | 19 | ? | 159-172 | 37-47 | ? |
| *r. rufulus* | 19 | 162-175 | 160-178 | 54-79 | 72-78 |
| *laevissimus* | 19(-21) | 172-181 | 172-183 | 58-69 | 76-81 |

### Lycodonomorphus bicolor (Günther)

1894b. *Glypholycus bicolor* Günther, Proc. Zool. Soc. London for 1893, p. 629, fig. 1: Shores of Lake Tanganyika.
1896d. Boulenger, p. 615.
1910a. Sternfeld, p. 15.
1915a. Boulenger, p. 201.
1915c. Boulenger, p. 619.
1924b. Loveridge, p. 4.
1929a. Werner, p. 50.
1933h. Loveridge, p. 232.
1933m. Witte, p. 86.
1937f. Loveridge, pp. 489, 496.
1941a. Uthmöller, p. 40 (as *Glypholicus*).
1947c. Laurent, p. 10.
1952. Witte, p. 18.
1953. Witte, p. 164, fig. 42.
1956. Laurent, p. 88, pl. ix, fig. 1.
1942b. *Nerophidion hypsirhinoidis* Werner, Sitzb. Akad. Wiss. Wien., **133**, Abt. 1, p. 54, fig. 7: No locality.
1928. Malcolm Smith, p. 496 (synonymizes with *bicolor*).

[3] 50-59 *fide* Laurent (1954b, p. 43).

[4] 59-71 *fide* Laurent (1954b, p. 43).

*Common Name.* Tanganyika White-bellied Water-Snake.

*Description.* Rostral broader than deep, well visible from above; nostril valvular, directed upwards in a semidivided nasal that is sometimes completely divided, rarely entire[5]; internasals narrow anteriorly, as long as, or longer or shorter than, broad, shorter than the prefrontals; prefrontals moderate; frontal 1¼ (usually 1½) to 2[6] times as long as broad, rarely[7] as long as its distance from the end of the snout, usually as long as its distance from the rostral, much shorter than the parietals; loreal longer than deep, in contact with, or separate from, the first labial, sometimes by the presence of a small scale[8]; eye small, pupil usually round, sometimes subelliptic[9]; preocular 1 (on both sides of all 111 snakes); postoculars 2 (110 ex.), very rarely 1 (M.C.Z. 54936); temporals 1+ 2 (both sides of 103 ex.), rarely 1 +1 (on one side only of M.C.Z. 54886) or 1 + 3 (M.C.Z. 54916, and on one side only of 6 others); lateral head shields separated by a deep groove from the upper labials; upper labials 7, 8 (eighth usually posterior to the gape) or 9 (left side of M.C.Z. 54879), the fourth, rarely fourth and fifth (M.C.Z. 54837, 54934, etc.) entering the orbit (67 ex.) or separated from it (at least on one side) by 1 or 2 minute suboculars, or by a subocular and an extension of the lower postocular (left side of M.C.Z. 54879), or by an extension of the preocular contacting the lower postocular (right side of M.C.Z. 54857); lower labials 8 or 9 (ninth usually posterior to the gape), first 4 (first 3 only on left side of M.C.Z. 54861 and 54921; or first 5 in M.C.Z. 54935 and on one side only in M.C.Z. 54921 and 54942) in contact with the anterior sublinguals, which are much longer than the posterior. Midbody scale-rows[10] 23-25 (23 in 109 snakes; 24 in 3, viz. M.C.Z. 54908 and 54940-1; 25 in 2, viz. M.C.Z. 54853 (♂)

[5] Entire in M.C.Z. 54851, 54919, or on left side only of 54852.

[6] Twice in M.C.Z. 54897.

[7] As long as its distance in M.C.Z. 26929, 54858, 54871.

[8] Small scale given off by 1st labial in M.C.Z. 30076, 54869, etc. Small scale given off by 2nd labial in M.C.Z. 54855, 54881, etc. Second labial transversely divided in M.C.Z. 54853, 54857, etc.

[9] Subelliptic in M.C.Z. 30076, 54859, 54916, and on left of 54941.

[10] 19, given by Boulenger (1915c, p. 619), due to inclusion of *whytii*; 21, stated in the original description, amended to 23 by Boulenger.

and 54924 (♀)); ventrals 152-166[11] (♂♂ 154-164; ♀♀ 152-166); anal entire; subcaudals[12] 52-71 (♀♀ 52-59; ♂♂ 63-71) pairs.

*Color.* Above, gray or plumbeous, rarely black, uniform except for the two or three outermost rows of scales which are white. Below, throat and belly white, uniform or occasionally some dusky flecking on the anterior third; tail white, sometimes uniform in young but usually with a dusky longitudinal line along the median sutures of the subcaudals.

*Size.* Largest ♂ (M.C.Z. 54854), 563 (420 + 143) mm.; largest ♀ (M.C.Z. 54902), 778 (615 + 163) mm.; smallest ♂ (M.C.Z. 54856), 227 (175 + 52) mm.; smallest ♀ (M.C.Z. 54852), 235 (188 + 47) mm. All from Kigoma, Tanganyika Territory.

*Sexual dimorphism.* This is reflected by their respective tail lengths, that of 52 ♂♂ being included in total length 3.64 to 4.42 times, with an average of 3.89; in 49 ♀♀ the tail was included in total length 4.32 to 5.06, with an average of 4.66. For the purpose of these figures snakes with incomplete tails were discarded. The number of subcaudals appear to be an even surer guide to sex, the ♀♀ having from 52 to 59, the ♂♂ from 63 to 71 pairs.

Compare with Laurent's (1956, p. 89) figures expressed as percentages with an average of .255 for ♂♂, .227 for ♀♀. None of his specimens attained the maximum size of those in the Museum of Comparative Zoology.

*Breeding.* A number of the ♀♀ taken at Kigoma between April 4 and May 4, 1956, are gravid. They have not been critically examined for precise dates and the number of eggs produced at a time.

*Diet.* I am indebted to Dr. E. Trewavas for determining the species of thirteen fish that Mr. C. J. P. Ionides removed from stomachs of these snakes, viz.

1 *Boulengerochromis microlepis* (Boulenger) from M.C.Z. 54892.

[11] 184, as given by Boulenger (1896d, p. 615) presumably a misprint. Battersby has recounted all British Museum *bicolor* and finds them within the range given for M.C.Z. material.

[12] 50 is the lowest given by de Witte (1952, p. 18), and Laurent (1956, p. 89), but the tail tips of all M.C.Z. snakes with less than 52 have been regenerated, though at times this is difficult to see. For ♂♂, Laurent gives 59-71.

1 *Haplotaxodon tricoti* Poll from M.C.Z. 54947.
1 *Lamprologus callipterus* Boulenger from M.C.Z. 54908.
2 *Lamprologus savoryi elongatus* Trewavas & Poll from M.C.Z. 54872 and 54922.
1 *Lamprologus* sp. from M.C.Z. 54916.
1 *Limnochromis pfefferi* (Boulenger) from I. 6773.
4 *Limnotilapia dardenii* (Boulenger) from M.C.Z. 54917, 54933, 54949.
2 *Stolothrissa tanganicae* Regan from I. 6773.

Witte (1952, p. 18) also mentions recovering a species of *Limnothrissa*. Except for a couple of cichlids, the stomach contents consisted of clupeids (Laurent:1956).

*Habitat.* C. J. P. Ionides informs me that he captured these *bicolor* in the lake at night by the light of a pressure lamp, taking the snakes in a hand net about the size of a shrimping net. Laurent (1956) says they are to be found hiding beneath stones on the lakeshore in the vicinity of rivers. He quotes N. Leleup who captured several in the burrows of gerbils (*Tatera* sp.) where they presumably pass the hours of daylight.

*Localities.* **Tanganyika Territory:** *Karema, Mpanda; Katabi near Bangwe; *Kigoma; Kirando Bay; Lagosa Bay; *Sumbawa. **Northern Rhodesia:** *Mpulungu. **Belgian Congo** — Tanganyika District: Kabimba Bay; Mtoto Bay; Pala Bay; Uvira. **Belgian Urundi:** Makamba (but considered doubtful by the collector); Rumonge.

*Range.* Lake Tanganyika off the coasts of Tanganyika Territory; Northern Rhodesia; Belgian Congo and Ruanda-Urundi.

### Lycodonomorphus subtaeniatus upembae Laurent

1933m. *Boaedon lineatus* Witte (part: not Duméril & Bibron), p. 86.
1953. Witte, p. 168.
1954b. *Lycodonomorphus subtaeniatus upembae* Laurent, Museo do Dundo, No. 23, p. 41, figs. 5-8: Nyonga, Katanga, Belgian Congo.

*Common Name.* Eastern Congo White-bellied Water-Snake.

*Description.*[13] Internasals shorter than the prefrontals; prefrontals moderate; frontal as long as, or shorter than, its distance from the end of the snout, much[14] shorter than the parietals;

[13] Taken entirely from the original description, where Laurent tabulates the scale-counts for the ♂ and all 21 ♀♀.

preocular 1 (41 sides), rarely 2 (3 sides); postoculars 2 (42 sides), rarely 1 (2 sides); temporals 1 + 2. Midbody scales with apical pits, in 21-23 rows; ventrals 172-188 (♂ 172; ♀♀ 175-188); anal entire; subcaudals 29-40 (♀♀ 29-34; ♂ 40).

*Color.* Above, coloring lighter than in *s. subtaeniatus* and the dark dorsal zone narrower; the two or three outermost rows of scales white.

*Size.* Only ♂ (ex Nyonga), 454 (387 + 67) mm.; largest ♀ (ex Nyonga), 831 (739 + 92) mm.

*Sexual dimorphism.* The solitary ♂ and one ♀ have 21 midbody scale-rows, the remaining 20 ♀♀ have 23 rows. The ♂ has fewer ventrals and more subcaudals than any of the ♀♀; also his tail is longer (♂ 15%; ♀♀ 10 to 12% of total length).

*Dentition.* Maxillary teeth 19-20.

*Localities.* **Belgian Congo:** Kina-Mwena; Nyonga near Lake Upemba.

*Range.* Southeastern Belgian Congo.

### Lycodonomorphus subtaeniatus subtaeniatus Laurent

1952b. *Boaedon virgatus* Laurent (not Hallowell), p. 199.

1954b. *Lycodonomorphus subtaeniatus subtaeniatus* Laurent, Museu do Dundo, No. 23, p. 38, figs. 1-4: Keseki, near Kwamouth, Belgian Congo.

*Common Names.* Western Congo White-bellied Water-Snake; *lubuebwe* or *lunoka* at Dundo, where the same names are applied to *Boaedon fuliginosus.*

*Description.*[15] Rostral broader than deep, just visible from above; nostril directed upwards in a semidivided nasal, internasals shorter than the prefrontals; prefrontals moderate; frontal as long as, or slightly longer or shorter than, its distance from the end of the snout, shorter than the parietals; loreal much longer than deep, separated from the first labial; preocular 1; postoculars 2; temporals 1 + 2; upper labials 8, fourth and fifth entering the orbit; lower labials 8, first 4 in contact with the anterior sublinguals, which are subequal to the posterior. Midbody scales with apical pits, in 21-23 rows (21 in 8 paratypes;

[14] 66-70% in *s. upembae* as against 74-86% in *s. subtaeniatus.*

[15] Based entirely on Laurent's admirable account of 5 ♂♂ and 8 ♀♀ as I have seen no material of this recently described species. For further details see Laurent's remarks.

23 in 5); ventrals 175-193 (♂♂ 175-180; ♀♀ 189-193); anal entire; subcaudals 41-58 (♀♀ 41-48; ♂♂ 52-58).

*Color.* Above, dark olive gray; flanks paler, usually bearing a longitudinal lateral band as dark as the dorsum but at times the two shades merge into one another; head with light lines analogous to those of *Boaedon fuliginosus* though not so clear and sometimes indistinct (for a detailed description of these markings consult original paper). Below, whitish, chin shield and first three lower labials marked with white, throat very slightly pigmented; tail with a dusky longitudinal line along the median sutures of the subcaudals.

*Size.* Largest ♂ (ex Keseki), 651 (529 + 122) mm.; largest ♀ (ex Dundo), 1009 (872 + 137) mm.

*Dentition.* Maxillary teeth 19-20.

*Hemipenes.* Hemipenis not bifurcate, extending to the level of the tenth or eleventh subcaudal; sulcus spermaticus forked near the sixth subcaudal; spines largest in the middle region, weakest at the base and towards the summit; no calyces. Laurent invites attention to the close resemblance of this hemipenis to that of *L. rufulus,* still more so to that of "*Glypholycus bicolor.*" He should be consulted for comments on its distinctness from *Lamprophis* and *Boaedon.*

*Sexual dimorphism.* Laurent points out that 5 of the 8 ♀♀ had 23 midbody scale-rows, whereas all the ♂♂ had 21. Seemingly significant in this species, though not so in *bicolor,* for dimorphism has progressed to the point where ♂♂ have fewer ventrals as well as more subcaudals; in addition, ♂ tails are always longer (♂♂ 22-24%; ♀♀ 14-17%).

*Diet.* A skink (*Mabuya* sp.) was recovered from the stomach of one of these snakes. This is especially interesting in view of the fact that *bicolor* is a fish-eater, while *rufulus* and its race appear to prey chiefly on amphibia.

*Localities.* **Angola:** Dundo. **Belgian Congo:** Kalina; Keseki near Kwamouth; Kunungu, Lac Leopold II; Leopoldville; Lomami; Luluabourg, Kasai.

*Range.* Western Angola to western Belgian Congo.

### Lycodonomorphus rufulus leleupi (Laurent)

1950b. *Ablabophis whytei leleupi* Laurent, Revue Zool. Bot. Afr., **43**, p. 351: Kundelungu (Irsac biological station), 1750 metres, northwest Lake Tanganyika, Belgian Congo.

1953. Witte, p. 165; figs. 43 a-e; col. pl. iii, fig. 3; pl. xvi, fig. 2.
1956. *Lycodonomorphus whytei leleupi* Laurent, p. 86.

*Common Name.* Congo Dark-bellied Water-Snake.

*Description.*[16] Rostral broader than deep, just visible from above; nostril directed upwards, between two nasals; internasals as long as, or longer or shorter than, broad, as long as, or shorter than, the prefrontals; prefrontals moderate; frontal as long as, or longer than, its distance from the end of the snout, shorter than the parietals; loreal longer than deep, well (only barely in 2 snakes) separated from the first labial, enters orbit on left side of one specimen (No. 34-54); preocular 1, rarely 2 (on only 3 out of 40 sides); postoculars 2; temporals 1 + 2 (34 sides) or 1 + 3 (14 sides); upper labials 8, fourth and fifth entering the orbit; lower labials 8, first 4 or 5 (6 sides only) in contact with the anterior sublinguals (anterior and posterior fused on right side of No. 112-122), which are subequal to the posterior. Midbody scale-rows 19 to 21 (19 in only 7 of the 24 snakes known); ventrals 164-174[17] (♂♂ 165-171; ♀♀ 164-174); anal entire; subcaudals (46-52 in type series, *fide* Laurent, but possibly tips regenerated) 52-67 (♀♀ 52-61; ♂♂ 65-67).

*Color.* Above, dark olive brown to glossy black, uniform (including outermost scale-rows). Below, anteriorly whitish to gray; belly of a 230 mm. juvenile is wholly white below, but larger young show progressively encroaching dark patches until the adult condition of a usually black belly sparsely flecked with cream is attained. One subadult from Kabwe River displays a more or less median black streak on its belly, while its tail, like those of the adults, is mostly black.

*Size.* Largest ♂ (I.R.B. 41-70), 540 (417 + 123) mm.; largest ♀ (I.R.B. 61), 851 (690 + 161) mm.; smallest ♀ (I.R.B. 4205-06), 230 (182 + 48) mm.

*Dentition.* Maxillary teeth 24; mandibular 24-27 (Laurent: 1956).

*Breeding.* On April 3, ova were small in a Lusinga ♀, but between June 14-18 five adults from the same locality held eggs ranging from 25 to 35 × 15 mm. Similarly were a gravid ♀

[16] Based on original description; plus 20 specimens, from 3 localities, each of which has been examined by me for every character cited.

[17] 162-174 *fide* Witte (1953 p. 167).

taken at Kabwe between May 21 and 25, and another on June 1 at Pelenge.

*Diet.* A young frog (*Hemisus* sp.) in one; in others various fish (*Barbus* sp. and *Kneria* sp.) *fide* M. Poll (Laurent:1956).

*Localities.* **Belgian Congo:** Kabwe River; Kundelungu; Lusinga; Mukelengia River; Pelenge River (for precise position of these places see Witte, 1953, p. 167 and end map).

*Range.* Montane streams from north end of Lake Tanganyika to region of Lake Upemba, Belgian Congo.

### Lycodonomorphus rufulus mlanjensis Loveridge

1953e. *Lycodonomorphus rufulus mlanjensis* Loveridge, Bull. Mus. Comp. Zool., **110**, p. 253: Ruo River, Mlanje Mountain, Nyasaland.
1953i. Loveridge, p. 476.

*Common Names.* Mlanje White-bellied Water-Snake (English); *chirumi* (Manganja).

*Description.*[18] Rostral broader than deep, just visible from above; nostril directed upwards, between two nasals; internasals as long as, or longer than, broad, slightly shorter than the prefrontals; prefrontals large, squarish; frontal as long as, or longer than, its distance from the end of the snout, shorter than the parietals; loreal longer than deep, well separated from the first labial; preocular 1; postoculars 2; temporals 1 + 2; upper labials 8, fourth and fifth entering the orbit; lower labials 8, first 4 in contact with the anterior sublinguals, which are subequal to the posterior. Midbody scale-rows 21; ventrals 163-169 (♂♂ 163-167; ♀ 169); anal entire; subcaudals 51-71 (♀ 51; ♂♂ 60-71).

*Color.* Above, glossy black; upper and lower lips white, the upper heavily infuscated, the lower only anteriorly so; the outermost scale-row and edges of the one next above it, whitish, more or less obscured with dusky infuscations. Below, faintly pinkish white; throat to anus immaculate except for an occasional tiny fleck (on three ventrals of type); tail with a longitudinal line formed of dusky median spots.

*Size.* Largest ♂ (M.C.Z. 51050:the type), 735 (550 + 180) mm., only known ♀ (B.M. 24.2.1.27), 780 (642 + 138) mm. The tail being 17% of her total length as against 21-24% for the three males.

[18] Based on 3 ♂♂ (from Mlanje and Cholo in M.C.Z.) and a ♀ (Zomba in British Museum).

*Remarks.* *L. r. mlanjensis* is distinguished from *rufulus* and all its races except *r. leleupi* of the Congo, by possessing 21 mid-body scale-rows. From *r. leleupi* (and *laevissimus*, of which two individuals with 21 scale-rows have been reported), it is readily distinguished by its immaculate white throat and belly. Whether additional Nyasaland material will demonstrate that it should be merged with *r. whytii* remains to be seen.

*Diet.* A large ranid tadpole was present in the stomach of the type.

*Parasites.* Nematode worms (*Kalicephalus* sp.; immature Ascaridae; also larval Anisakinae, probably *Cleoascaris* sp.) were abundant in the type.

*Temperament.* Even Africans appear to recognize the docility of this species as will be seen from their attitude as described by Loveridge (1953e, p. 255).

*Habitat.* Apparently hide beneath stones in shallow streams.

*Localities.* **Nyasaland:** *Muyenda Stream, an affluent of Nswadzi River, Cholo Mountain; *Ruo River, Mlanje Mountain; *Zomba Mountain.

*Range.* Montane streams of southern Nyasaland.

### Lycodonomorphus rufulus whytii (Boulenger)

1897e. *Glypholycus whytii* Boulenger, Proc. Zool. Soc. London, pp. 800, 802, pl. xlvi, fig. 2: Fort Hill, Nyasaland.
1898. Johnston, p. 361a.
1915e. Boulenger p. 619.
1929a. Werner, p. 50.
1935. *Ablabophis whytii* Cott, p. 965.
1940. Bogert, p. 18.
1952. *Ablabophis rufulus whytei* Ionides, *in* Swynnerton, p. 10.
1953e. *Lycodonomorphus rufulus whytii* Loveridge, pp. 255, 317.
1953i. Loveridge, p. 476.
1955e. Loveridge, p. 182.

*Common Name.* Whyte's Water-Snake.

*Description.*[19] Rostral broader than deep, just visible from

[19] Based on ♀♀ (from Bungwe; Songea and Fort Hill) and Cott's Charre snake which is too dried and shrivelled to be of much good; however its tail with 37 subcaudals does *seem* to be intact. Cunha's two snakes from Massangulo, Portuguese Nyasaland, reported as *Ablabophis rufulus*, were actually *Boaedon fuliginosus*.

above; nostril directed upwards, between two nasals; internasals as long as, or longer than, broad, shorter than the prefrontals; prefrontals moderate; frontal as long as, or longer than, its distance from the end of the snout, shorter than the parietals; loreal longer than deep, well separated from the first labial; preoculars 1-2; postoculars 2; temporals 1 + 2; upper labials 8, fourth and fifth entering the orbit (or 9, with fifth and sixth entering on right side of Charre ♀) lower labials 8, first 4 in contact with the anterior sublinguals, which are subequal to the posterior. Midbody scales without apical pits, in 19 rows; ventrals 159-168 (all ♀ ♀; 172 — not 176 as given by Cott — if Charre snake included); anal entire; subcaudals 46-47 (all ♀ ♀; 37-47 if Charre snake included).

*Color.* Above, dark olive to slate gray, uniform, or the outermost scale-row on either side pinkish or yellowish white. Below, pinkish or yellowish white, uniform (Fort Hill), or a few dusky patches down the middle of the venter (Rungwe), or a dusky median line commencing on the throat, rapidly broadening to occupy all but the lateral edges of the ventrals and subcaudals.

*Size.* Largest ♀ (M.C.Z. 52637), 709 (590 + 119) mm. from Songea; Rungwe ♀ (A.M.N.H. 38984), 625 (519 + 106) mm.; Fort Hill type ♀ (Brit. Mus.), 565 (465 + 100) mm.

*Dentition.* Maxillary teeth apparently 24 on one side of damaged Rungwe snake (*fide* Bogert).

*Sexual dimorphism.* Tails of these 3 ♀ ♀ are from 15-17% of total lengths.

*Diet.* Hind feet of an amphibian in stomach of Rungwe snake (Bogert); hind limbs of a *Rana fuscigula* in the Songwe specimen.

*Parasites.* The entire digestive tract of the Songwe snake was riddled with worms. These have been identified by J. T. Lucker as a ♀ Oxyuroidea besides both sexes of a *Kalicephalus*, probably *K. micrurus*. In the mesentery were two ♂ *Dracunculus* sp. and numerous encapsuled larvae of one of the Physalopteridae.

*Localities.* **Tanganyika Territory:** Rungwe Mountain; *Songea boma. **Nyasaland:** *Fort Hill. **Mozambique:** *Charre (if referable to this race).

*Range.* Southern Tanganyika Territory and northern Nyasaland, south (? down eastern side of Lake Nyasa) to the Zambezi at Charre, Mozambique.

## Lycodonomorphus rufulus rufulus (Lichtenstein)

1823. *Coluber rufulus* Lichtenstein, Verz. Dubl. Zool. Mus. Berlin, p. 105: South Africa.
1826. Fitzinger, p. 57.
1831. *Coronella leucopilus* A. Smith, S. African Quart. Jour. (1), No. 5, p. 17:
1837. *Coronella rufula* Schlegel (part), p. 74, pl. ii, figs. 18-19.
1843. Traill, p. 136 (as in Schlegel, subcaudal counts in error).
1843. *Lycodonomorphus rufula* Fitzinger, p. 27.
1861. Fitzinger, p. 408.
1847. *Lamprophis rufulus* A. Smith, pl. lviii.
1863a. Jan, p. 285.
1866. Jan, pl. iv, fig. 1.
1884a. Müller, p. 284.
1887b. Boettger (part), p. 161 (omit Clarkebury).
1887h. Boulenger, p. 177.
1889. Boettger, pp. 290, 294.
1890. Müller, p. 693.
1891a. Matschie, p. 609.
1892a. Boulenger, p. 176.
1854a. *Ablabes rufula* Duméril & Bibron, p. 308.
1858c. Günther, p. 30.
1867a. Steindachner, p. 62.
1893b. *Ablabophis rufulus* Boulenger, p. 318.
1898. Boettger, p. 35.
1898. Werner, p. 143.
1898. Selater, p. 98.
1902. Lampe & Lindholm, p. 17.
1905h. Boulenger, p. 255.
1907j. Boulenger, p. 486.
1907c. Roux, p. 733.
1908b. Boulenger, p. 228.
1908. Gough (part), p. 21.
1908. Odhner, p. 5.
1910b. Boulenger, p. 503.
1910a. Hewitt, p. 57.
1910b. Sternfeld, p. 15.
1910a. Werner, p. 355.
1912. FitzSimons, F.W., pp. 82, 91.
1912. Hewitt, p. 267.
1913. Hewitt & Power, p. 161.
1916. Andersson, p. 40.

1925b. Flower, p. 966.
1929. Flower, p. 181.
1929. Rose, pp. 146, 157, figs. 91-94, 102.
1929a. Werner, p. 48.
1931. Power, pp. 43, 48.
1935. Power, p. 333.
1937e. Hewitt, p. 57, pl. xviii.
1940. Bogert, p. 18.
1946a. FitzSimons, V.F., p. 355.
1950. Fantham & Porter, pp. 601, 603.
1950. Rose, pp. 225, 269, 272, 320, figs. 140-143, 164.[20]

Further citations of "*rufulus*" will be found under *laevissimus* and *Boaedon f. fuliginosus*.

*Common Names.* Brown Water-Snake (Hewitt). It has also been called Olive-brown Water-Snake by F. W. FitzSimons, South African Rufous Snake by Flower, Black Water Snake by Rose.

*Description.* Rostral broader than deep, just visible from above; nostril directed upwards, between two nasals; internasals as long as, or longer than, broad, much shorter than the prefrontals; prefrontals moderate; frontal 1½ to 1⅔ times as long as broad, as long as its distance from the end of the snout, shorter than the parietals; loreal longer than deep, well separated from the first labial; preocular 1, rarely 2; postoculars 2; temporals 1 + 2; upper labials 8, fourth and fifth entering the orbit; lower labials 8, first four in contact with the anterior sublinguals, which are subequal to the posterior. Midbody scales with or without apical pits, in 19 rows; ventrals 160-178 (♂♂ 162-175; ♀♀ 160-178); anal entire; subcaudals 54-78[21] (♀♀ 54-79; ♂♂ 72-78).

*Color.* Above, dark olive brown to glossy black, uniform, or the outermost scale-row on either side slightly yellowish white;

[20] Largely a reprint of 1929, and repeated in 1955, pp. 28, 90, 178 as *Lycodonomorphus rufulus*.

[21] 84 *fide* Boettger (1889).

upper and lower lips (light pink in life) lemon to ochre or yellowish white, immaculate. Eyes dark brown flecked with reddish brown, the pupil edged with reddish brown. In young snakes the back and sides are a deep yellowish brown, the underside a paler immaculate yellow than in the adults.

Below, anteriorly yellowish white becoming brighter yellow towards the anus; tail yellow, usually immaculate, occasionally with a dusky median line (*fide* Günther: 1858; Boettger: 1889; Müller: 1890b; their specimens coming from Natal; Botschabelo near Middleburg, Transvaal; and Harrismith, Cape Province, respectively), or each scale dark-edged.

*Size.* Largest ♂ (A.M.N.H. 60113), 605 (445 + 160) mm.; largest ♀ (M.C.Z. 21306), 827 (635 + 192) mm.; smallest, a ♂ (M.C.Z. 55143), 269 (205 + 64) mm.

*Remarks.* The type of *rufulus* is presumably still in the Berlin Museum, while that of *leucophilus* is unknown. Rochebrune's (1884a, p. 158) listing of this species from Senegal is omitted as obviously erroneous. The two snakes from Massangulo, Portuguese Nyasaland, referred to *rufulus* by Cunha (1935, p. 5; 1937, p. 1779) were actually based on *Boaedon l. lineatus*, so Dr. A. A. Themido tells me. The scale counts furnished by Cunha are not those of his specimens but were taken from Boulenger's (1893b, p. 318) catalogue.

*Dentition.* Maxillary teeth 25 on right rami of both Merebank snakes, the six foremost ones slightly less recurved than those following; posterior teeth somewhat smaller (Bogert).

*Hemipenes.* Hemipenis bifurcate at extreme end, extends to the level of the tenth subcaudal; sulcus spermaticus forked at the sixth subcaudal; spines feebly enlarged at the base, arranged in diagonal rows or, towards distal end, in chevrons, those on the terminus of each lobe decreasing in size.

*Sexual dimorphism.* Verified subcaudal counts for ♀ ♀ is 54-73; in ♂ ♂ 72-78 (possibly to 84 if Boettger's Botschabelo snake was a ♂ and the count correct). Intact tails of 9 ♀ ♀ are 19-23% of total length; those of 3 ♂ ♂ are 26-28% of total length.

*Breeding.* In December about 6 (photo shows 9) eggs are laid, from which emerge six-inch young (Rose).

*Longevity.* Four years, 3 months, 10 days, in London Zoo (Flower).

*Diet.* They have been seen to chase frogs into water and, diving in after them, seize the hapless amphibian on the bottom (F. W. FitzSimons). *Xenopus l. laevis* was found in one's gullet (Werner:1898), and *Rana g. rhodesiana* in a stomach (V. FitzSimons:1939b). Frogs are said to be invariably swallowed head first, and photographs of one being engorged, with subsequent x-ray of it in the snake's stomach, are furnished by Rose (1929: figs. 91-94). On exhibition in the Transvaal Museum is a *r. rufulus* with the head of a frog (*Rana f. fuscigula*) in its greatly distended mouth. V. FitzSimons told me that this snake, rather than relinquish its captive, had allowed itself to be anesthetized in this position. Another exhibit was of a *r. rufulus* that had died while attempting to swallow a fish that was too large for it (Loveridge). In captivity some fed on barbel, carp and tinned sardines (Fantham & Porter:1950); other captive *r. rufulus* seized live fish which they held by as many as five coils (F. W. FitzSimons). They will attack and kill by constriction other snakes that may be confined in the same vivarium (C. J. French in Hewitt).

Following the sweeping statement (1950; p. 269) that this species subsists "mainly, if not entirely, on frogs," Rose (1955, p. 90) goes to the other extreme, adding that it consumes tadpoles in large quantities and, though in his experience "it will not touch" toads, "it will readily eat mice and geckos." On what evidence this last surprising statement is based, is not mentioned.

*Parasites.* Fantham and Porter (1950) found nematodes (*Ophidascaris mombasica*) in the small intestine, from whose lower reaches and cloaca they described three new protozoa (*Balantidium serpentis; Chilodon cyprini serpentis; Nyctotherus ophidiae*). Hemogregarines were present in the blood.

*Habitat.* Restricted by their diet to marshy ground or the vicinity of swamps, pools, and rivers. In clear mountain streams

they may be seen lying on the sandy or gravelly bottom where, if disturbed, they seek shelter beneath stones by forcing their way through the soft sand or gravel. By day they may be found under stones in damp spots (Hewitt) or hiding beneath rotten logs lying on muddy ground beside a stream (V. FitzSimons). At night some were captured in partially dried stream beds where they were apparently engaged in hunting frogs (Power), but in districts such as Kimberly that are subject to drought, the Brown Water-Snake is not to be found (Hewitt & Power).

*Localities.* **Southern Rhodesia:** Matabeleland (1893); Vumba Mtn.* (M.C.Z.). **Bechuanaland. Transvaal:** Bethel*; Boekenhoutkloof*; Botschabelo; Brits*; Broederstroom*; Bronkhorstspruit*; Driefontein; Entabeni*; Haenertsburg*; Irene*; Johannesburg*; Lake Fundusi*; Lydenburg*; Majielsberg; Mariepokop*; Middleburg*; Modderfontein*; Mphome; Pietersburg; Pinedene*; Potchefstroom*; Pretoria* (M.C.Z.); Rustenberg*; Tzaneen*; Wakkerstroom*; Waterberg District*; Watervaalboven*; White River*; Witbank*; Woodbush*. **Natal:** Durban; Giants Castle*; Merebank; Port Natal; Sibudeni; Vryheid*; Zululand. **Orange Free State:** Modder River*; Parys*; Tweespruit*. **Basutoland. Cape Province:** Albany District*; Algoa Bay*; Avontuur*; Burghersdorp; Cape Flats; Clanwilliam; De Wet*; George; Gnadenthal (Jan, 1863); Grahamstown; Grootvadersbosch; Harrismith; Kingwilliamstown; Knysna; Linokana; Pondoland; Port Elizabeth; Port St. Johns (M.C.Z.); Prince Albert; Robben Island; Schoester's Drift (M.C.Z.); Somerset Strand; Stellenbosch; Table Mountain; Touw's River; Worcester*. **Southwest Africa:** Damaraland (Palgrave coll. in S.A.M.).

*Range.* Africa south of the Zambezi River (in well-watered regions).

### Lycodonomorphus laevissimus (Günther)

1862b. *Natrix laevissima* Günther, Ann. Mag. Nat. Hist., (3) **9**, p. 124, pl. ix, fig. 4: "probably from East Indies" (error).
1937e. Hewitt, p. 58.
1937b. Mertens, p. 12.

* Specimens in the Transvaal Museum whose identifications have been checked for the purpose of this revision by Dr. V. FitzSimons.

1863. *Neusterophis laevissima* Günther, p. 16, footnote.
1887b. *Lamprophis rufulus* Boettger (part: not Lichtenstein), p. 161.
1893b. *Tropidonotus laevissimus* Boulenger, p. 226.
1908b. Boulenger, p. 228.
1909f. Boulenger, p. 944.
1910b. Boulenger, p. 503.
1912. FitzSimons, F.W., p. 82.
1912. Hewitt, p. 267.
1925. Werner, p. 49.
1929a. Werner, p. 24.
1898. *Grayia lubrica* Sclater, Ann. S. African Mus., 1, pp. 99, 109, pl. —, fig. 1: Tsomo, Transkei District, Cape Province.
1908. *Ablabophis rufulus* Gough (part: not Lichtenstein), p. 21.
1923c. *Hydrablabes melanogaster* Werner, Ann. Naturhist. Mus. Wien, 36, p. 161: "Tenimber Island," Dutch East Indies (error).
1940. *Neusterophis laevissimus* Bogert, pp. 5, 34.
1946b. FitzSimons, V.F., p. 379.
1950. Rose, p. 272.
1955. Rose, p. 92.

*Common Names.* Dusky-bellied Water-Snake (which I suggest as being more diagnostic than either "Watermeyer's Black Snake," proposed by F. W. FitzSimons, or "Black Water Snake," put forward by Hewitt); *ixilenzi* (Kaffir:Hewitt).

*Description.* Rostral broader than deep, just visible from above; nostril directed upwards, between two nasals; internasals longer than broad, shorter or longer than the prefrontals; prefrontals small, sometimes pointed anteriorly; frontal 1⅔ to 2 times as long as broad, shorter than, as long as, or longer than, its distance from the end of the snout, shorter than the parietals; loreal longer than deep, in contact with the first labial or, rarely, separated from it by a granule; preocular 1; postoculars 2; temporals 1 + 2; upper labials 8, fourth and fifth entering the orbit; lower labials 8, first 4 in contact with the anterior sublinguals, which are subequal to the posterior. Midbody scales without apical pits, in 19 rows, exceptionally 21;[22, 23] ventrals 172-183 (♂♂ 172-181; ♀♀ 172-183); anal entire, rarely divided[22]; subcaudals 57-78 or 81.[23]

[22] Only in a Port Elizabeth snake recorded by Mertens (1937b).

[23] Only in a Lothair snake which FitzSimons (1946b) thinks may be subspecifically distinct.

*Color.* Above, grayish olive to glossy black; from the eye to above the gape there is usually a more or less well-defined yellowish white line; upper and lower labials and two outermost scale-rows on either side yellowish white, generally spotted or blotched with grayish black.

Below, yellowish white with a narrow, dusky median line or series of spots extending from the throat to end of tail, occasionally broadening posteriorly even to the exclusion of the yellowish white.

*Size.* Total length of holotype ♂ (Brit. Mus.), 850 (650 + 200) mm., largest ♀ (A.M.N.H. 18223), 1100 (875 + 225) mm., while a ♀ without precise locality measured (*fide* Werner:1925), 1050 (850 + 200) mm.

*Remarks.* The unlocalized type is in the British Museum; the type of *G. lubrica*, collected by M. Watermeyer, in the South African Museum, the type of *H. melanogaster* in Vienna. It was synonymized by Werner himself, who explained the wrong locality as due to the practice of attaching the data-bearing label to the easily transposed stoppers of the museum jars.

*Habits.* Almost entirely aquatic.

*Habitat.* Fairly common in streams and reservoirs around Grahamstown (Hewitt) where, as at Kingwilliamstown, *L. r. rufulus* also occurs.

*Localities.* **Transvaal:** Ermelo District: Lothair (but 21 scale-rows). **Natal. Cape Province:** Alicedale; *Blaauwkrantz; Bushmans River; *Clarkebury; Emfundisweni; *Grahamstown; Kingwilliamstown; Pirie; Tsomo, Transkei District.

*Range.* Transvaal south to Natal, west to eastern Cape Province (i.e. west to Graaf Reinet and south to Port Elizabeth).

## Genus NATRICITERES Loveridge[24]

1953e. *Natriciteres* Loveridge, Bull. Mus. Comp. Zool., **110**, p. 248. Type by original designation: *Coronella olivacea* Peters.

*Definition.* Maxillary teeth 23-25, the anterior ones subequal, the last 3 or 4 sharply increasing in size; mandibular teeth

[24] The eight generic names that have been misapplied to snakes of this genus will be found listed under the original (1953e) description of *Natriciteres* (i.e. ♀ *Natrix* + *teres* = smooth).

slightly increasing in size towards the middle of the jaw, decreasing posteriorly. Head slightly distinct from neck; eye moderate, with round pupil; nostril more or less directed upwards, in a divided nasal; a loreal; preoculars 1-2; lateral head shields not separated by a groove from the upper labials.

Body cylindrical; scales smooth, without apical pits, in 15-19 rows; ventrals rounded; anal entire or divided. Tail moderate, tapering; subcaudals paired. Hemipenis of male basally bifid, exhibiting a short secondary lobe; sulcus spermaticus not forked. Hypapophyses present posteriorly in the vertebral column.

Additional characters common to the five members of the genus are: Rostral broader than deep, visible from above; nostril between two nasals or separated from the posterior one by a narrow rim; internasals more or less narrowly truncate anteriorly, about as long as broad, slightly shorter than, or as long as, the prefrontals; frontal (in the middle) 1⅔ to 2 (2⅓ occasionally in *o. olivacea*) times as long as broad, longer than its distance from the end of the snout, shorter than the parietals; loreal about as long as deep.

*Range.* Africa south of 15° N., i.e. Sudan east to Somalia, south to Southern Rhodesia, northwest through Belgian Congo to French Guinea.

### *Key to the Species of Natriciteres*

1. Anal divided[25] . . . . . 2
   Anal entire . . . . . 5

2. Midbody scale-rows 19 (rarely 17 or 18); range: swampy lowlands of Sudan, east to southern Somalia, south to Southern Rhodesia,[26] northwest through the Belgian Congo to French Guinea . . . . . *o. olivacea* (p. 29)
   Midbody scale-rows 17 or less (rarely 18 or 19) . . . . . 3

3. Midbody scale-rows 17 (very rarely 15, 18 or 19); range: montane marshes and forest fringes of East Africa from Tanganyika Territory south through Mozambique, Nyasaland and Northern Rhodesia

[25] Entire in one of two juvenile *o. olivacea* from Yakoma-Abiras in the Paris Museum (*fide* Guibé).

[26] On the basis of the solitary Salisbury record of 1898.

to Southern Rhodesia and Angola ..... *o. ulugurnensis* (p. 37)
Midbody scale-rows 15 (or at times 17 in *pembana*) ..... 4

4. Subcaudals 49-63; range: an insular form found only on Pemba Island, north of Zanzibar Island ..... *o. pembana* (p. 42)
Subcaudals 63-78; range: French Cameroon west to French Guinea ..... *variegata* (p. 43)

5. Subcaudals 75-95; midbody scale-rows invariably 17 correlated with an entire anal; range: Belgian Congo northwest to French Guinea ..... *fuliginoides* (p. 46)

It will be noted that the ranges of these last two species are coextensive and both kinds may occur in the same locality. In color and pattern they are indistinguishable, a conspicuous light nuchal collar being present in both, yet they appear to be distinct species.

In the following tabulation parentheses have been used to indicate unusual variations detected during the examination of over 200 snakes.

In the following tables the forms are arranged according to their maximum size, which exhibits some correlation with an increase in the number of ventrals and subcaudals. Many lower subcaudal counts, including some of my own, have appeared in the literature. On re-examination, however, these are found to have been based on individuals with abbreviated tails, *whose pointed terminal tips have been regenerated.* When lost early in life these are sometimes so astonishingly like the original as to have misled distinguished herpetologists into describing as new species examples of such short-tailed snakes. In the genus *Natriciteres* detection is complicated by the high percentage — varying from locality to locality, but possibly 30% to 50% — of adult snakes that have lost their tail tips to predators, as can be seen by comparison with the tails of young specimens.

## STATISTICAL DATA FOR THE SPECIES OF *NATRICITERES*: AMENDED TO 1957.

| Species or race | Pre-ocular | Post-oculars | Temporals | Upper Labials | Lower Labials | Midbody Scale-rows |
|---|---|---|---|---|---|---|
| *o. pembana* | 1 2 | 3 | 1+2 | 8 | 8 | 15(17) |
| *variegata* | 1 2 | (2)3 | (1+1)1+2 | (7)8(9) | 8-9 | (13)15(17) |
| *o. ulugurucnsis* | 1(2) | (2)3 | (1+1)1+2(2+1) | 8(9) | 8-10 | (15)17(19) |
| *o. olivacea* | 1(2) | (1)(2)3 | (1+1)1+2(1+3) | (7)8(9) | 8-10 | (17-18)19 |
| *fuliginoides* | 1-2 | (2)3 | (1+1)1+2(0+2) | (7)8 | 8-10 | 17 |

| Species or race | Ventrals | Anals | Subcaudals | Maximum length in ♂♂ | Maximum length in ♀♀ |
|---|---|---|---|---|---|
| *o. pembana* | 123-128 | 2 | 49-63 | 200+ 78 mm. | 210+ 75 mm. |
| *variegata* | 124-137 | 2 | 63-78 | 265+135 mm. | 240+101 mm. |
| *o. ulugurucnsis* | 125-144 | 2 | 62-84 | 300+130 mm. | 350+140 mm. |
| *o. olivacea* | 128-149 | 2 | [27]51-87 | 332+132 mm. | 460+144[28] mm. |
| *fuliginoides* | 122-137 | 1 | 75-95 | 370+186[28] mm. | 310+ ? mm. |

[27] 51 in U.S.N.M. 49023 whose tail-tip may possibly be regenerated; 54, recorded by Fischer (1884b) for a Masailand snake, is presumably in the same category; this leaves 57 as the lowest authentic count.

[28] In neither of these instances is the tail measurement that of the snake whose body length is given as the maximum for the form.

## Natriciteres olivacea olivacea (Peters)

1854b. *Coronella olivacea* Peters, Monatsb. Akad. Wiss. Berlin, p. 622: Tete, Zambezi River, Mozambique.
1855. Peters, p. 52.
1858c. Günther, p. 39.
1866a. Bocage, p. 47.
1866b. Bocage, p. 66.
1882a. Bocage, p. 288.
1882a. Peters (part), p. 114, pl. xvii, fig. 1 (omit Angola & Zanzibar coast).
1882b. Müller, p. 168.
1887b. Mocquard, p. 66.
1888. Mocquard, p. 128.
1889. Pfeffer, p. 9.
1893b. Boettger, p. 123.
1893. Pfeffer, p. 79.
1899. Mocquard, p. 219.
1908b. Mocquard, p. 558.
1860a. *Coronella* (*Meizodon*) *dumerilii* Günther, Proc. Zool. Soc. London, p. 429, fig. —: "Sierra Leone" i.e. Gold Coast, *fide* Boulenger.
1863a. *Enicognathus punctatostriatus* Jan, Arch. Zool. Anat. Fisiol., **2**, p. 278: No locality (Type in Hamburg Museum).
1866. Jan, pl. iv, fig. 4.
1877c. *Coronella* (*Mizodon*) *olivacea* Peters, p. 614.
1888a. Boettger, p. 84.
1877c. *Neusterophis atratus* Peters, Monatsb. Akad. Wiss. Berlin, p. 614, pl. —, fig. 1: Chinchoxo, Cabinda.
1888a. Günther, p. 51.
1884a. *Zacholus olivaceus* Rochebrune, p. 156 (ignored in this revision).
1884a. *Meizodon dumerilii* Rochebrune, p. 158 (ignored in this revision).
1886. *Grayia Giardi* Dollo, Bull. Mus. Roy. Hist. Nat. Belgique, **4**, p. 158, figs. 1-2: Lake Tanganyika region, Belgian Congo.
1894a. Boulenger, p. 288.
1910a. Sternfeld, p. 23.
1893b. *Tropidonotus olivaceus* Boulenger, p. 227.
1896d. Boulenger, p. 604.
1896e. Boulenger, p. 216.
1896. Peracca, p. 2.
1896. Tornier, p. 67.
1897b. Boulenger, p. 278.
1897c. Boulenger, p. 800.
1897g. Boulenger, p. 279.

1897. Tornier, p. 67 (reprint of 1896 book).
1897b. Tornier, p. 65.
1898. Boettger, p. 22.
1898. Johnston, p. 361a (not in 1897 ed.).
1898. Sclater, p. 98.
1898. Tornier, p. 292.
1900b. Boulenger, p. 451.
1900. Flower, p. 968.
1902d. Boulenger, p. 446.
1905e. Boulenger, p. 112.
1907a. Boulenger, p. 10.
1907a. Roux, p. 76.
1908a. Sternfeld, p. 404.
1908b. Sternfeld, pp. 211, 228.
1908c. Sternfeld, p. 243.
1908. Werner (1907), p. 1866.
1908a. Werner, p. 170.
1909b. Boulenger, p. 303.
1909. Peracca, p. 172.
1909a. Sternfeld, p. 11.
1909b. Sternfeld, p. 10.
1910b. Boulenger, p. 503.
1910. Peracca, p. 3.
1910. Roux, p. 98.
1910a. Sternfeld (part), p. 14, fig. 12.
1911. Lampe, p. 187.
1911. Sternfeld & Nieden, p. 385.
1912. Hobley, p. 47.
1912. FitzSimons, F. W., p. 82.
1912c. Sternfeld, p. 265.
1913. Boettger, pp. 345, 347, 353.
1915a. Boulenger, p. 201.
1915c. Boulenger, p. 619.
1915d. Boulenger, p. 645.
1916f. Chabanaud, p. 368.
1916a. Loveridge, pp. 77, 82.
1917b. Chabanaud, p. 10.
1917. Sternfeld, p. 460.
1918a. Loveridge, p. 334.
1919a. Boulenger, p. 276.
1919g. Boulenger, p. 19.

1919d. Chabanaud, p. 567.
1921a. Angel, p. 42.
1922. Aylmer, p. 15.
1923e. Loveridge (part), p. 876.
1924b. Loveridge, p. 4.
1927d. Witte, p. 321.
1929a. Werner, pp. 15, 24.
1933. Schouteden, p. 236.
1933j. Witte, p. 122.
1933m. Witte, p. 85.
1934a. Schwetz, p. 382.
1937b. Monard, p. 113.
1894c. *Coronella olivacea* var. *dumerilii* Günther, p. 87.
1897. Johnston, p. 362.
1898. Johnston, p. 361a (reprint of 1897 book).
1895a. *Mizodon olivaceus* Bocage, p. 74.
1896a. Bocage, p. 91.
1897b. Mocquard, p. 8.
1923. *Natrix olivacea* Schmidt (as *olivaceous*), p. 58.
1925a. Loveridge (part), p. 71.
1928e. Barbour & Loveridge (part), p. 109.
1928. Cott, p. 953.
1928g. Loveridge (part), p. 34.
1928j. Loveridge (part), p. 71.
1929. Flower, p. 174.
1929h. Loveridge (part), p. 19.
1929. Worthington, p. 124.
1933f. Angel, p. 72, figs. 25-25a.
1933h. Loveridge (part), p. 231.
1934e. Mertens, pp. 78, 171.
1934. Pitman, p. 293.
1935a. Corkill, p. 14.
1935. Cott, p. 964.
1941. Moreau & Pakenham, p. 108.
1943. Scortecci, p. 270.
1951. Monard, p. 147.
1936h. *Natrix olivacea olivacea* Loveridge, p. 21.
1936j. Loveridge, p. 236.
1936. Pitman, p. 224, pl. iii, fig. 4; pl. B, fig. 2.
1937c. Loveridge, p. 270.
1937f. Loveridge, pp. 489, 493, 496.
1938b. Mertens, p. 46.

1938a. Pitman, pp. 301, 326.
1938b. Pitman (repaged reprint embracing 1936 and 1938a in book form).
1938. Uthmöller, p. 42.
1939a. Scortecci, p. 270.
1941a. Uthmöller, p. 26.
1941b. Uthmöller, p. 230.
1947. Pakenham, p. 138.
1940. *Neusterophis olivaceus olivaceus* Bogert, p. 35.
1941. Witte, p. 173.
1942e. Loveridge, p. 261.
1942. Moreau & Pakenham, p. 62.
1949a. Parker, p. 28.
1950f. Laurent, p. 128.
1953. Witte, p. 160, fig. 40.
1945. *Neusterophis olivaceus* Leeson, p. 3.
1950. Ionides, p. 100.
1950. Leeson, pp. ix, 36, 38, 66, 136.
1950. Rose, pp. 272, 320.
1950a. Villiers, p. 39.
1950b. Villiers, p. 69, figs. 71-72.
1954. Dekayser & Villiers, p. 963.
1955. Rose, pp. 92, 178, fig. 1.
1953e. *Natriciteres olivacea olivacea* Loveridge, pp. 251, 317.
1954b. Laurent, p. 44 (as *olivaceus*).
1955. Witte, p. 214.
1956. Laurent, p. 132, fig. 21.
1954d. *Natriciteres olivaceus* Laurent, p. 305.

Further references to "*olivacea*" or "*olivaceus*" will be found under its subspecies *ulugurucnsis* and *pembana*.

*Common Names.* Olive Marsh-Snake (preferred A. L.), many names have been proposed beginning with Black-backed Grass-Snake (Flower, 1929), Grass-Snake; Olive Grass-Snake; Olive Water-Snake; Black-backed Water-Snake; and Common Water-Snake; *inkubayoka* (Nyarwanda: *fide* Laurent).

*Description.* Preoculars 1, rarely 2; postoculars 3, rarely 1 or 2; temporals 1 + 2, rarely 1 + 1 or 1 + 3; upper labials 8, rarely 7 or 9, the fourth and fifth, rarely the third, fourth and fifth, or fourth, fifth and sixth, or fifth and sixth, entering the orbit; lower labials 8-10, the first four, five, or six in contact with the

anterior sublinguals, which are much shorter than the posterior. Midbody scale-rows 19, rarely 18 or 17; ventrals 128-149 (130-147 in M.C.Z.); anal divided; subcaudals (? 51, 52) 57-87.

For characters common to all species, and tabulated data, see pp. 25-26, 28.

*Color.* Above, olive brown, brown, gray, or bluish black; upper lip yellowish, the labial sutures black; juvenile specimens sometimes exhibit a pale spot on the parietals; usually a more or less distinct darker, sometimes chocolate, vertebral band four or five scales in width, bordered on either side by a narrow buffy one or, more rarely, by a series of light dashes or dots; the coloring of the flanks impinging as olive, gray, pale blue, red, or bright mauve on the ends of the ventrals, which are otherwise yellowish (sometimes orange in life) occasionally edged with black.

Pitman (1936, p. 225) comments on the handsome coloring of many of the snakes taken around Lakes Bunyonyi (6,400 feet), Chahafi and Mutanda (6,000 feet), whose black-edged, dark brown, vertebral band is flanked by narrower bands of bright chestnut with paler edges; beyond this again is a narrow dark line below which is a broad band of mauve or reddish chestnut occupying most of the lower flank. His book should be consulted for further notes on coloration. The wide range of ventral coloring is quite irrespective of sex.

Laurent (1956, p. 134) mentions a red-eyed albino juvenile from Bukavu; also a Kitutu specimen that is black below.

*Size.* Length of ♂ (M.C.Z. 40329), 464 (332 + 132) mm., of largest perfect ♀ (M.C.Z. 40334), 553 (409 + 144) mm., both from Ngatana, but surpassed in head and body length by a ♀ (M.C.Z. 40317) of 585+ (460 + 125+) mm. with regenerated tail-tip.

*Remarks.* The type of *Coronella dumerilii* Günther (1860) was said to have a single anal and to have come from Sierra Leone. I mention this as *N. fuliginoides* has a single anal and does occur in Sierra Leone. However, Boulenger (1893, pp. 227-228) synonymized *dumerilii* with *olivacea* (which has a divided anal) and changed its locale to Gold Coast, donor H. H. Evans. Only

one specimen is listed. J. C. Battersby informs me (29.v.50) that it was one of five snakes received from H. Evans of the Gold Coast (now Ghana).

Sternfeld's (1917) record of seven *olivacea* from Duma with entire anals is surely a lapsus, for in both ventral and midbody scale-rows they agree with *olivacea*. The scale-rows on an Albertville snake (M.C.Z. 30074) reported as 17 by me (1933h), are actually 19 at mathematical midbody. The four Magrotto Mountain snakes with 19 rows brought to me (1942e) by natives, may well have come from the cultivated areas lower down the mountain as the half-dozen snakes I personally captured at the forest-edge all have 17 rows.

*Sexual dimorphism.* This is so slight as to be negligible, for example in M. C. Z. material examined in 1950:

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| ventrals of | 26 ♂♂ | ranged from | 130-141, | giving an | average | of | 134.9 |
| " | 38 ♀♀ | " | " | 131-147, | " | " | " | " 137.7 |
| subcaudals of | 17 ♂♂ | " | " | 57-80, | " | " | " | " 69.1 |
| " | 19 ♀♀ | " | " | 51-80, | " | " | " | " 76.2 |
| tail lengths | 17 ♂♂ | " | " | 43-56% | of the total length | | | 47.8% |
| | | | | 36-51% | " | " | " | 43.8% |

For these last two characters fewer snakes were available owing to the large number whose tails were truncated or regenerated.

*Breeding.* Typical *olivacea* produces more eggs than its montane race.

On February 14, at Kaimosi, a ♀ held 6 eggs measuring 23 x 7 mm.

On February 19, at Kaimosi, a ♀ held 6 eggs measuring 23 x 7 mm.

Between June 11-20, at Ngatana, a ♀ held 6 eggs measuring "small"

Between June 11-20, at Ngatana, a ♀ held 6 eggs measuring 15 x 6 mm.

Between June 11-20, at Ngatana, a ♀ held 6 eggs measuring 19 x 7 mm.

Between June 11-20, at Ngatana, a ♀ held 6 eggs measuring 19 x 11 mm.

Between June 11-20, at Ngatana, a ♀ held 6 eggs measuring 22 x 10 mm.

Between June 11-20, at Ngatana, a ♀ held 6 eggs measuring 23 x 11 mm.

On June 15 at Dar es Salaam, a ♀ laid 8 eggs measuring 17 x 8 mm.,

this last lot possibly prematurely as it was shortly after capture.

*Diet.* This captive snake swallowed two *Rana a. fuscigula* hindlegs first on June 22, and another headfirst on June 24. Remains of a *Rana* sp. in a Witu snake; *Phrynobatrachus* sp. in a Duem specimen (Werner, 1908); *Phrynobatrachus minutus* in both a Kaimosi and a Mwaya snake; *Hyperolius milnei* at Golbanti; *Leptopelis argenteus* at ? Morogoro; *Bufo steindachneri* on four occasions at Laini and Ngatana; fish in an Ngatana snake also. According to Pitman (1934) an Olive Marsh-Snake has been seen swallowing locust hoppers, while Corkill (1935a) mentions caterpillars in the Sudan.

*Parasites.* Cestodes and Pentastomida (now U.S.N.M. 47029) were present in an Mtimbuka snake.

*Defensive tactics.* A gentle snake, never biting, but relying on a nauseous odor (Laurent:1956). When captured, according to Pitman (1934), this small snake exhibits considerable truculence but soon becomes tame and confiding in captivity. My own impression is of violent struggling to get free which they often achieve by the loss of their tails. Only once was I personally responsible for such a loss. Having grabbed a snake by the tail, I continued holding it while getting a bag in which to drop the reptile, but its violent wriggling resulted in its breaking away, leaving the tail in my grasp. As it is also quite usual to find members of the genus *Grayia* with truncated tails, it would seem probable that aquatic snakes are more liable to seizure by waders or other waterfowl than are more terrestrial types, and by active wriggling they frequently achieve liberty by sacrificing their tails. In some localities they doubtless suffer from attacks by other predators such as turtles or fish.

*Habitat.* Though principally a lowland reptile, typical *olivacea* occurs up to 6400 feet in the undulating uplands of Central Africa. Schmidt (1923) has suggested this is a savanna species that has recently invaded the Congo forests; actually the Olive Marsh-Snake is a forest-edge, rather than a sylvicoline, form, occurring in clearings and open glades. More usually, however,

*olivacea* is found in moist situations such as, for example, beneath grass strewn on the floor of a watcher's hut in a rice swamp; beneath grass and reeds piled around the edges of native plots adjacent to a river; one was hoed up in grassland near the lakeshore, another had sought shelter beneath a bundle of thatching beside an unfinished hut (Loveridge). Two were found beneath the movable gangway of a pier by Pitman, who remarks that this marsh-snake will readily dive to hide beneath subaqueous vegetation. I once observed a marsh-snake swimming across the Tana River at a point where it was fifty yards across; on reaching the north bank the reptile paused to rest.

*Localities.* **Sudan:** Bahr el Jebel; *Bo River; Duem; Lake No; *Mongalla; Wau; White Nile south of Khartoum. **Ethiopia:** Lake Rudolf. ? **French Somaliland:** Côte des Somalis (Paris Mus.).[29] **Somalia:** Mogadiscio **Uganda:** *Bukatakata; Busu Hill; Damba Island; Entebbe; Fort Portal; *Gulu; Ibanda, Toro; Kaianja, Lake Edward; *Katwe; Kitala; Lake Bunyonyi; Lake Chahafi; Lake Edward; Lake Kyoga (Kioga); *Lake Mutanda; Lake Victoria; Lalle, Lake Kyoga; Lugasi near Kampala; Mitiana; Mjanji; *Mushongero; Nansere, Masaka; Sesse Islands. **Kenya Colony:** *Belazoni; *Golbanti; *Kaimosi; Kakamega; Kenya Mountain; *Laini; Lake Rudolf; *Mkonumbi; *Ngatana; Peccatoni; Pokomonie; *Witu; Yala River. **Tanganyika Territory:** Arusha; Bukoba; *Dar es Salaam; *Ikiju, Musoma; Ipiana; *Kabare; *Kigoma; Kilimanjaro Mtn.; Kingani; *Kipangate, Lake Rukwa; Klein Popo; Kome Id.; Madimula, Usaramo; *Magrotto Mtn. (foot of ?); Makindo River; *Morogoro; *Mwaya; *Ujiji; *Ukerewe Id. **Zanzibar Island:** Kokotoni; Zanzibar. **Mafia Island. Mozambique:** Angoche; Fambani; Quilimane; Rikatla; Tete; Zambezi Expedition. **Nyasaland:** Fort Hill; Karongwa to Kondowe; Lake Nyasa; *Mtimbuka; Nkata Bay to Ruarwe; "Nyika Plateau." **Northern Rhodesia:** *Abercorn; Kazungula; Lealui; Mpulungu; Petauke; Shambanza's, Nausenga River; *Wantipa, Lake Mweru; Zambezi Plains. **Southern Rhodesia:** Salisbury. **Angola:** Dundo; Malange (Malanji);

[29] The inclusion of Somaliland in the range by Boettger (1888a) was apparently due to the title of Mocquard's (1888) paper, but Mocquard clearly states that his single specimen came from Zanzibar. The listing of this species from Somaliland by Boulenger (1897g) was based on his (1896e) own identification of a snake from Lake Rudolf.

Muita River; north of Kwanza River; Pungo Ndongo (Adungo; Andongo). Possibly some are referable to *o. uluguruensis*. **Cabinda:** Chinehoxo. **Belgian Congo:**[30] *Albertville; Banana; Beni; Bitshumbi (Vitshumbi); Boma; Bugasia, Lake Edward; Dika; Elisabethville; *Idjwi Island; Kabare, Lake Edward; Kabengere; Kabunda; Kakyelo; Kamanda, Lake Edward; Kando; Kanonga River; Kapolowe; Kasai River; Katanda; Kiambi; Kikondja; Kumungu; Lake Tanganyika; Lofoi; Lukula; Mabwe River; Maji (May) ya Moto; Makaia Ntete; Manda; Mangbatta (Monbuttu); Mati; Medje; Mokabe-Kasari; Musosa; Mutsora; Niangara; Nyonga; Parc Albert; Poko, Upper Uele; Pweto; Rungu; Ruwindi; Stanleyville; Tembwe; Zaire = Congo River; Zambi. **Ruanda-Urundi:**[31] Bukavu; Kissenji; Muleria region. **French Congo:** Brazzaville; confluence of Dougon and Kibali Rivers; Gabon; Lambarene; Loango; Passa River region, affluent of Ogoone River; Yakoma-Abiras, Upper Oubanghi. **French Cameroon:** Garua. **British Cameroon:** Isongo (specimen re-examined by Mertens:1938b). **Nigeria:** Brass; *Lagos. **Dahomey:** Widah. **Togoland:** Kete; Misahöhe. **Ghana:**[32] Achimota School (probably). **Ivory Coast:** Bouafle. **French Guinea:** Beyla. **West Africa:** Abadafi (not located. Müller:1885b).

*Range.* Sudan, east to Somalia, south to Mozambique, west through Southern Rhodesia to Angola, north and west to French Guinea.

### Natriciteres olivacea uluguruensis (Loveridge)

1882a. *Coronella olivacea* Peters (part), p. 115 (specimens with 17 scale-rows).

1884a. Fischer, p. 6 (Masailand snake with 17 scale-rows).

1894a. *Coronella olivacea* var. *dumerilii* Günther, p. 618 (Zomba Mtn.; material now in Brit. Mus. exhibits 17 scale-rows).

1896d. *Tripodonotus olivaceus* Boulenger (part), p. 604 (Zomba and Mlanje Mtns.).

[30] For precise localization of Congo localities, see the respective articles by Witte and Laurent.

[31] For 30 additional localities, mostly in Ruanda-Urundi, see Laurent (1956, pp. 133-134).

[32] The type of *dumerilii* Günther, originally said to come from Sierra Leone (hence its listing from there by Aylmer:1922) was later stated by Boulenger (1893b) to have come from the Gold Coast = Ghana.

1910a. Sternfeld (part), p. 14 (Amani, though possibly 19 scale-rows).
1911b. Nieden, p. 442 (Amani).
1913b. Werner, p. 717 (Amani).
1923c. Loveridge (part), p. 876 (Bagilo, though with 19 scale-rows).
1925a. *Natrix olivacea* Loveridge (part), p. 71 (Bagilo).
1928c. Barbour & Loveridge (part), p. 109 (all except Dar es Salaam).
1933h. Loveridge (part), p. 231 (Rungwe Mtn. only).
1939b. FitzSimons, V. F., p. 20 (Silinda Mtn.).
1935. *Tropidonotus* sp., Cunha, p. 4 (Massangulo, Niassa, with 15 scale-rows).
1935. *Tropidonotus fuliginoides* Cunha (not Günther), p. 3 (Massangulo).
1937. Cunha (1935), p. 1778.
1941. Themido, p. 16 (Massangulo).
1937b. Monard, pp. 113, 115 (Kalukembe, Angola).
1935c. *Natrix olivacea uluguruensis* Loveridge, Bull. Mus. Comp. Zoöl., **79**, p. 7: Nyange, Uluguru Mountains, Tanganyika Territory.
1937f. Loveridge, p. 502.
1941a. Uthmöller, p. 42.
1947. Pakenham, p. 138.
1940. *Neusterophis olivaceum uluguruensis* Bogert, p. 35.
1942a. Loveridge, p. 261.
1953e. *Natriciteres olivacea uluguruensis*, Loveridge, pp. 252, 318.
1953h. Loveridge, p. 143.
1955e. Loveridge, p. 181.
1955e. Loveridge, p. 181.
1956c. Loveridge, p. 42.

*Common Names.* Montane Marsh-Snake (English); *nyoka usambia* (Sambara, but not specific).

*Description.* Preocular 1, rarely 2; postoculars 3, rarely 2; temporals 1 + 2, rarely 1 + 1, 1 + 2 or 2 + 2; upper labials 8, very rarely 9, the fourth and fifth, or very rarely the third, fourth and fifth, or fourth, fifth and sixth, entering the orbit; lower labials 8-10, the first 4 or 5 in contact with the anterior sublinguals, which are much shorter than the posterior. Midbody scale-rows 17, rarely 15 or 19; ventrals 125-144[33] (♂♂ 125-140, ♀♀ 130-144); anal divided; subcaudals 62-84 (♀♀ 62-77; ♂♂ 66-84).

[33] 144 for a Zomba snake (B.M. 48.1.1.87) confirmed by J. C. Battersby. If Fischer's (1884a) Masailand snake really had 17 midbody scale-rows, presumably it was an aberrant *o. olivacea*, judging by its 148 ventrals and 54 subcaudals (?intact). Cunha's (1935) counts are rejected as probably not being those of the Massangulo snake, which I have examined. Its ventrals were 135, not 153 as stated.

For characters common to all species, and tabulated data, see pp. 25-26, 28.

*Color.* Above, olive brown, brown, gray, or bluish black; upper lip yellowish, the labial sutures black; usually a more or less distinct darker, sometimes chocolate, vertebral band, bordered on either side by a narrower buffy one two scales wide, or rarely by a series of light dashes or dots; the coloring of the flanks impinging as olive, gray, pale blue, red, or bright mauve on the ends of the ventrals, which are otherwise yellowish (in life creamy white, bright yellow, deep orange) though sometimes edged with black.

The wide range of ventral coloring is quite irrespective of sex.

*Size.* Length of ♂ (M.C.Z. 23129), 430 (300 + 130) mm., from Nyingwa, *ca.* 7500 feet, the highest point at which any were taken; on the other hand, the largest ♀ (M.C.Z. 23118), 490 (350 + 140) mm., was from Nyange, only 2500 feet.

*Remarks.* The snake from Massangulo referred to *Tropidonotus* sp. by Cunha (1935 and 1937) agrees in all respects with known variants of this race except in its ventral count of 153 (a transposition for 135). For example M.C.Z. 44110 from Ugano, Matengo Mountains, just north of Massangulo, has 15 midbody scale-rows, 2 preoculars, and 1 + 2 temporals, while others from the same locality have 17 scale-rows, 1 preocular, and 1 + 1 temporals. Moreover, Cunha (1935 and 1937) records three other snakes from Massangulo as *fuliginoides* because they have 17 scale-rows. Through the courtesy of Dr. Themido, who reprinted Cunha's list in 1941, I have been able to examine one of these snakes and find it is unquestionably an *o. ulugurensis* with divided anal.

It might be as well to add that the scale-counts and color descriptions given by Cunha (1935) are *not* those of his specimens but translations from Boulenger's catalogues into Portuguese, which later (1937) he retranslated back into English!

Barbour & Loveridge (1928c) furnished scale-counts around neck, midbody, and preanal region, for sixty-two montane snakes. These counts were made by a student; the subcaudal range, given as 63 to 87, I have since amended to 62-84.

*Dentition.* See Bogert (1940).

*Anatomy.* The hemipenis is described by Bogert (1940).

*Sexual dimorphism.* This is so slight as to be negligible, as the following figures will show:

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| ventrals of | 40 ♂♂ | range from | 125-140, | giving an | average of | 134.9 | | |
| " | 58 ♀♀ | " | " | 130-148,[34] | " | " | " | " 136.5 |
| subcaudals | 21 ♂♂ | " | " | 66-84, | " | " | " | " 74.8 |
| " | 28 ♀♀ | " | " | 62-77, | " | " | " | " 69.6 |
| tail length | 21 ♂♂ | " | " | 48-61%, | " | " | " | " 53.3% |
| " | 28 ♀♀ | " | " | 43-54%, | " | " | " | " 50.0% |

The last, or tail length, character, is expressed as a percentage of total length, for which only half the total number of snakes were available as exactly half of these reptiles had truncated or regenerated tail tips.

*Breeding.* Apparently these montane snakes lay fewer eggs than the lowland form.

On July 22, at Bagilo, a ♀ held 3 eggs measuring 22 x 6 mm.

October 8, at Nyange, a ♀ held slightly developed eggs 5 mm. in diam.

October 9, at Nyange, a ♀ held 2 eggs measuring 12 x 6 mm.

November 19, at Amani, a ♀ held 4 eggs measuring 20 x 8 mm.

November 25, at Amani, a ♀ held 4 eggs measuring 16 x 7 mm.

November 29, at Amani, a ♀ held 4 eggs measuring 21 x 8 mm.

But during November the majority of females held undeveloped ova.

*Diet.* Three snakes held frogs (*Arthroleptis s. lönnbergi* and *A. xenodactylus*); another eight frog's eggs; a fifth stomach contained three round white eggs, apparently a frog's but 4.5 mm. in diameter; there was a caterpillar in a sixth.

*Parasites.* Nematodes (*Kalicephalus microrus*) in a Nyange snake, while in one Amani ♀ were *Kalicephalus* sp., *Ophidascaris* sp., and *Amplicaecum africanum*. A Magrotto snake held an indeterminate nematode but it is unusual for snakes of this race to be infected.

*Enemies.* A Cape File-Snake (*Mehelya c. capensis*) captured near Lujeri River, Mlanje Mountain, disgorged the tail of a Mon-

[34] These figures (130-148) are my own counts; 148 occurs in a snake (M.C.Z. 53662) from Achimota, Ghana, as well as in one (M.C.Z. 54057) from Abercorn, Northern Rhodesia.

tane Marsh-Snake. A Vine-Snake (*Thelotornis k. kirtlandii*) was observed swallowing another in a vivarium from which several marsh-snakes had already disappeared.

*Defensive tactics.* When seized by the tail this little snake wriggles violently until its caudal appendage breaks off. The tail-tip is missing from 41 of the 108 snakes I have examined, and the suggestion it is not only predators that are responsible is scarcely warranted by the incidence of loss as between the sexes.

*Habitat.* Though not primarily a forest species, this snake is frequently to be found beneath fallen bark or logs lying at the forest edge where congenially moist conditions are present. In native plots they conceal themselves in piles of rubbish or under stones. Marshy spots and the banks of streams are visited in search of small frogs, and after heavy rain these reptiles are sometimes found on paths.

I should have said that in tropical East Africa this race was essentially a montane form characterized by 17 midbody scale-rows, though at Amani (3000 feet) and on adjacent Magrotto Mountain examples with 19 scales are not uncommon. Recently, however, at Liwale (2100 feet), Mr. C. J. P. Ionides has collected abundant material of this race and found that 19 rows do not occur there, but 10% of those examined (i.e. 3 out of 28) possess 15 midbody scale-rows; such individuals also crop up in series from Songea and the Matengo Mountains.

*Localities.* **Tanganyika Territory:** *Liwale; Magrotto Mtn. —*Magrotto; Matengo Mtns.—*Ugano; *Mbeya; *Rovuma River; Rungwe Mtn.—*Nkuka Forest; *Songea; Tukuyu; Uluguru Mtns.—*Bagilo, *Mkangazi, *Nyange, *Nyingwa, *Vituri; Usambara Mtns.—*Amani; *Bumbuli. **Mozambique:** Massangulo. **Nyasaland:** *Cholo Mtn.; Mlanje (Milangi) Mtn.; Tengadzi River; Zomba Mtn. **Northern Rhodesia:** Fwambo. **Southern Rhodesia:** Selinda Mtn.—*Chirinda Forest. **Angola:** Kalukembe.

*Range.* Chiefly montane forests and marshes of Tanganyika Territory, south through northeast Mozambique to Southern Rhodesia, west to Angola.

### Natriciteres olivacea pembana (Loveridge)

1925a. *Natrix olivacea* Loveridge (part), p. 71.
1935e. *Natrix olivacea pembana* Loveridge, Bull. Mus. Comp., **79**, p. 8: Chakechake, Pemba Island, north of Zanzibar Island.
1937f. Loveridge, p. 493.
1941. Moreau & Pakenham, p. 108.
1941a. Uthmöller, p. 42.
1947. Pakenham, p. 138.

*Common Name.* Dwarf Marsh-Snake.

*Description.* Preoculars 1-2; postoculars 3; temporals 1 + 2; upper labials 8, third, fourth and fifth, or fourth and fifth, entering the orbit; lower labials 8, the first 4 in contact with the anterior sublinguals, which are much shorter than the posterior.[35] Midbody scale-rows 15-17; ventrals 123-128 (for ♂♂ alone, consequently for both sexes); anal divided; subcaudals 49-63.

For characters common to all species, and tabulated data, see pp. 25-26, 28.

*Color.* Above, uniform brownish olive; upper lip yellowish, the labial sutures black; flanks olive *only slightly* impinging on the ends of the ventrals, which are otherwise yellowish.

*Size.* Length of ♂ (M.C.Z. 46125), 278 (200 + 78) mm., from Wete; length of holotype ♀ (M.C.Z. 19112), 285 (210 + 75) mm., from Chakechake.

*Sexual dimorphism.* There is no difference between the sexes in ventral counts, both ranging from 123-128, and only an average difference (♀♀ 49-56; ♂♂ 52-63) in the number of subcaudals, more marked in tail length expressed as a percentage of total length, viz. 32-35% for three ♀♀, 36-43% for three ♂♂ possessing apparently intact tails.

*Remarks.* For a detailed study of midbody lepidosis consult Pakenham (1947) where he points out that of eleven snakes he collected, only three had 15 midbody scale-rows, the rest having 17. However, he finds Pemba snakes are consistently recognizable in possessing 15 rows in the preanal region, while Zanzibar reptiles (which he regards as *o. olivacea* with some intermediates with *o. uluguruensis*) invariably display 17, or an occasional 16, in this region.

[35] Except in M.C.Z. 46126, which is abnormal on one side.

In mainland populations of *o. uluguruensis* from southeast Tanganyika Territory I have encountered five examples with 15 midbody scale-rows; these were from Liwale (3), Songea (1), and Ugano (1), in every instance the snake being one of a much larger number of typical *uluguruensis*.

*Habitat.* Of five snakes captured at Wete by Mr. R. H. W. Pakenham, three were taken beneath coconut husks in shade, one under a tussock in a grassy field, and one beneath a piece of wood in swampy ground.

*Localities.* **Pemba Island:** *Chakechake; *Wete.

*Range.* Pemba Island, Indian Ocean, is separated from the African mainland by a channel of exceptional depth — 400 fathoms, i.e. eight times as deep as the shallow sea between Zanzibar and the adjacent coast of Tanganyika with which it was united in geologically recent times. However, the habits of this marsh-snake make transportation with agricultural produce possible.

## Natriciteres variegata (Peters)

1861a. *Mizodon variegatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 358: Pel, Ghana.
1902b. Mocquard, p. 415.
1893b. *Tropidonotus variegatus* Boulenger, p. 217.
1893c. Matschie, p. 211.
1895f. Boulenger, p. 33.
1896d. Boulenger, p. 603.
1898. Boettger, p. 19.
1901. Schenkel, p. 156.
1908a. Sternfeld, pp. 404, 421.
1908b. Sternfeld, pp. 211, 218.
1909a. Sternfeld, p. 10.
1909b. Sternfeld, p. 10.
1916f. Chabanaud, p. 368.
1919a. Boulenger, p. 276.
1921a. Chabanaud, p. 467.
1921b. Chabanaud, p. 523.
1922. Aylmer, p. 18.
1929a. Werner, p. 21.
1897b. *Tropidonotus fuliginoides* Werner (?part, with 15 scales), p. 402.
1930a. *Natrix fuliginoides* Barbour & Loveridge (not Günther), p. 772.

1936h. Loveridge (part), p. 21.
1933f. *Natrix variegatus* Angel, p. 75, figs. 26-26a.
1951. Monard, p. 147.
1941c. *Neusterophis variegatus* Loveridge, p. 120.
1945. Leeson, p. 1.
1950. Leeson, pp. ix, 36, 66, 134.
1950b. Villiers, p. 69, figs. 69-70.
1951. Villiers p. 40.
1954. Angel, Guibé, Lamotte & Roy, p. 386.
1954. Dekeyser & Villiers, p. 960.
1954b. Villiers, p. 1237.

Further citations of "*variegatus*" will be found under *fuliginoides*.

*Common Name.* Variable Marsh-Snake.

*Description.* Preoculars 1-2; postoculars 2-3; temporals 1 + 2, rarely 1 + 1[36]; upper labials 8, rarely 7 or 9,[37] the fourth and fifth, rarely the fourth only, entering the orbit; lower labials 8-9, the first 4 in contact with the anterior sublinguals, which are much shorter than the posterior. Midbody scale-rows 15, rarely 13[38] or 17[39]; ventrals 124-137[40] (♂♂ 124-135; ♀♀ 127-140); anal divided; subcaudals 63-78 (♀♀ 63-75; ♂♂ 73-78[41]).

For characters common to all species, and tabulated data, see pp. 25-26, 28.

*Color.* Above, dark brown to brick red; end of snout and anterior portion of parietals paler; upper lip yellowish, the labial sutures black; nuchal collar white, more or less edged with black; an ill-defined dark or brownish gray vertebral band present in young, often absent in adults; flanks brown with a dorso-lateral series of whitish dots, the brown impinging on the ends of the otherwise white ventrals, occasionally in the form of a series of dark spots.

[36] On right side only of a Suracoco ♂ (M.C.Z. 52218).

[37] Nine on right side only of a Somanya snake (M.C.Z. 55378).

[38] 13 in an Nzebela snake (*fide* Chabanaud: 1921a).

[39] 17 in an Nzo snake (C.M. 1943-81, *fide* Angel et al:1954).

[40] Verified counts of M.C.Z. material are 124-135, but Angel et al record five higher, viz. 136 (2 snakes), 137 (2) and 140 (1). The type was said to have 143, possibly due to a transposition of figures?

[41] Verified counts of M.C.Z. material are 64-74; both 63 (for a ♀) and 73 (for two ♂♂) are based on Mt. Nimba snakes (Angel et al:1954).

*Size.* Length of ♂ (M.C.Z. 49692), 400 (265 + 135) mm., from Mampong; length of a ♀ (M.C.Z. 22502), 341 (240 + 101) mm. The unsexed type (Leyden Mus.) was only 328 (222 + 106) mm.

*Remarks.* My (1936h) action in synonymizing *variegatus* with *fuliginoides* because both, with identical coloring, occur at Bitye, was ill-advised in view of the fact that 15 scale-rows is correlated with a divided anal in all fifteen *variegatus* subsequently studied by me, whereas 17 scale-rows and a single anal characterize the eight *fuliginoides* in the Museum of Comparative Zoology. Later I (1942e) pointed out they should be regarded as full species because of the considerable overlap in their distribution. Leeson's (1945) key errs in assuming the preoculars always number 2; this is the case in eight of our snakes, but only 1 preocular is present in six others.

*Sexual dimorphism.* There is no difference in ventral counts as between the sexes and only an average difference (♀ ♀ 64-76; ♂ ♂ 75-78) in the number of subcaudals; the difference is more marked in tail length expressed as a percentage of the total length, viz. 50-56% for six ♀ ♀, 60% for all four ♂ ♂ with tails intact.

*Diet.* A frog in one Paiata snake.

*Parasites.* A linguatulid (*Porocephalus subulifer*) from a Tafo snake was identified for me by Dr. H. R. Hill (5.ix.50).

*Enemies.* Chabanaud (1921a) comments on the tail being intact in only 1 of 8 snakes from French Guinea. It is truncated in only 6 of the 17 specimens (chiefly Ghanian) in the Museum of Comparative Zoology.

*Localities.* **French Cameroon:** *Bitye; Yaunde. **Nigeria:** Asaba. **Togoland:** Kete; Misahöhe; *Worawora. **Ghana:** Aburi; *Achimota; *Khong, Volta River; *Kumasi; *Mampong; *Oda; Pel; *Somanya; *Tafo. **Ivory Coast:** Banco Reserve; Bossou; Gama; Keoulenta; Nzo (17 scales!); Serengbara; Tonkoui Mtn.; Ziela; Zonguepo. **Liberia:** *Bandaja; *Bolahun; Bromley; Gibi; *Piata (Paiata; Peahtah); *Suacoco. **French Guinea:** Beyla; Kerouane; Kouroussa; Macenta; Nimba Mtn.; Nzebela; Nzerekore; Sampouyara. **Sierra Leone:** (*fide* Aylmer).

*Range.* French Cameroon west to French Guinea.

## Natriciteres fuliginoides (Günther)

1858c. *Coronella fuliginoides* Günther, Cat. Snakes Brit. Mus., p. 39: West Africa.
1889. Mocquard, p. 143.
1896. Günther, p. 264.
1863d. *Meizodon longicauda* Günther, Ann. Mag. Nat. Hist., (3) **12**, p. 352, pl. v, fig. A: Fernando Po.
1875a. Peters, p. 198.
1884a. Rochebrune, p. 158 (ignored).
1887a. Bocage, p. 184.
1884a. *Zacholus fuliginoides* Rochebrune, p. 156 (ignored).
1887b. *Coronella longicauda* sp. n. Mocquard, Bull. Soc. Philom. Paris, (7) **11**, p. 69: Franceville, French Congo (restricted by A.L.).
1890. *Coronella* (*Meizodon*) *variegata* Müller (not Peters), p. 692.
1893b. *Tropidonotus fuliginoides* Boulenger, p. 217.
1896d. Boulenger, p. 603.
1897. Sjöstedt, p. 24.
1897b. Werner (part), p. 402.
1898. Boettger, p. 19.
1898a. Werner, p. 212.
1899a. Werner, p. 135.
1900b. Boulenger, p. 451.
1902a. Werner, p. 343.
1905f. Boulenger, p. 185.
1906i. Boulenger, p. 211.
1908a. Sternfeld, pp. 404, 421.
1908b. Sternfeld, pp. 211, 227.
1909a. Sternfeld, p. 10, figs. 12-13.
1909b. Sternfeld, p. 10, figs. 10-11.
1909d. Werner, p. 247.
1910. Müller, p. 595.
1911. Lampe, p. 186.
1915a. Boulenger, p. 201.
1917a. Phisalix, p. 335.
1917. Sternfeld, p. 459.
1919a. Boulenger, p. 276.
1921a. Chabanaud, p. 467.
1921b. Chabanaud, p. 523.
1922. Aylmer, pp. 15, 18.
1927d. Witte, p. 321.
1929a. Werner, p. 21.
1933m. Witte, p. 85.

1895a. *Mizodon fuliginoides* Bocage, p. 75.
1895c. Bocage, p. 13.
1896b. Mocquard, p. 45.
1897b. Mocquard, p. 8.
1903a. Bocage, p. 42.
1929. *Natrix fuliginoides* Flower, p. 174.
1933f. Angel (part), p. 74 (omit Yakoma Abiras specimens).
1940a. Mertens, p. 241.
1951. Monard, pp. 147, 157.
1940. *Neusterophis fuliginoides* Bogert, p. 33, fig. 3.
1945. Leeson, p. 2.
1950. Leeson, pp. ix, 36, 38, 66, 135.
1950b. Villiers, p. 69.
1953. Witte, p. 159, fig. 39.

Further citations of "*fuliginoides*" will be found under *olivacea uluguruensis* and *varicgata*.

*Common Names.* Collared Marsh-Snake (Loveridge); Smoky Snake (Flower).

*Description.* Preoculars 1-2; postoculars 2-3; temporals 1 + 2, rarely 0 + 2 or 1 + 1[42]; upper labials 8, rarely 7, the fourth and fifth entering the orbit; lower labials 8-9,[43] the first 4 or 5 in contact with the anterior sublinguals, which are much shorter than the posterior. Midbody scale-rows 17[44]; ventrals 122-137[45]; anal entire; subcaudals 75-95.[46]

For characters common to all species, and tabulated data, see pp. 25-26, 28.

*Color.* Above, brown; end of snout and most of parietals paler; upper lip yellowish, the labial sutures usually black; nuchal collar white to buff, more or less heavily edged with black; dorsum very rarely exhibiting indistinct traces of a darker vertebral band; flanks brown with occasionally a dorsolateral series

[42] 0 + 2 in an aberrant Metet snake (Bogert :1940); 1 + 1 on left side only of a Kribi reptile (M.C.Z. 7845).

[43] Allegedly 11 in a cotype of *longicauda* Mocquard (1887b).

[44] Allegedly 19 in a Congo snake (Bocage :1887a); possibly an *olivacea?*

[45] Allegedly 117 (*fide* Angel :1933f), or 119 for a Franceville snake and 137 for a Kerouane specimen (*fide* Guibé in litt. 8.ix.50).

[46] Allegedly 57 in a Congo snake (Bocage :1887a); possibly an *olivacea?* Sexed material too scanty to justify giving sexual ranges.

of whitish dots, the brown impinging on the ends of the otherwise white ventrals that are sometimes edged with brown or black.

*Size.* Length of ♂ (M.C.Z. 9265), 468 (282 + 186) mm. from Lolodorf, but surpassed in snout to anal length by a ♂ (A.M.N.H. 45927) with a head and body measurement of 370 mm., its tail, like that of the largest recorded ♀ (A.M.N.H. 50552) of 310 mm., being truncate.

*Remarks.* Mocquard (1887b) comments on the fact that the tails are intact in only 2 of his 6 cotypes, and later (1897b) in only 2 out of 8 snakes. Boulenger (1893b; 1896d) records intact tails in only 5 of the 12 specimens in the British Museum. The tails are intact in 2 of the 8 examples in the Museum of Comparative Zoology.

*Sexual dimorphism.* There is no difference in ventral counts as between the sexes, and truncated tails preclude speculation about the subcaudals or relative tail lengths.

*Dentition.* See Bogert (1940).

*Anatomy.* Parotids are present according to Phisalix (1917a). The hemipenis is well figured, described, and discussed by Bogert (1940).

*Diet.* A frog (*Rana masecareniensis*) in stomach of a Cameroon frog (Werner, 1897b).

*Habitat.* Frequently seen on bush paths in Sierra Leone according to Aylmer (1922). Sternfeld (1908b), however, is mistaken in saying these snakes are confined to the coast. This author comments on the occurrence of all three species in the Cameroons, but whereas *fuliginoides* is there the most abundant and rare in Togo, the situation in Togo is reversed for *variegatus* (27 specimens) is plentiful and *fuliginoides* scarce.

*Localities.*[47] **Belgian Congo:** Albertville; Arebi; Butu-Polo; Ganda-Sundi; Kabwe; Kai-Bumba; Kapanga; Kenia Stream, affluent of Lusinga River; Kisala; Kumungu; Lofoi; Lower Congo; Lukolela; Lukonzolwe; *Makaia Ntete; Mubale-Munte; Sandoa; Tembwe; Temvo; Upoto. **French Congo:** Abiras; Alaima Leketi; Franceville; Gabon; Lambarene; Loudinia-Niari; Mayombe (Maïjombe or Majumba); Ogoone. **Rio Muni:** (as Spanish Guinea). **Fernando Po:** Musola; Natividad; Sao Carlos. **French**

[47] Angolan records of snakes with 17 midbody scale-rows have divided anals and are consequently referable to *o. ulugurucnsis.*

**Cameroon:** Baga near Konn; Bipindi; Dehane; Dibongo near Edea; Dipikar; Itoki; Jengwe; Josplatte; *Kribi; Limbe; *Lolodorf; Lonji; Metet; Molunda (Molundu); Pungo Songo; *Sakbayeme. **British Cameroon:** Bibundi; Buea; Buenga-Vorwerk, Moliwe Plantation; Isongo; Johann Albrechtshöhe; Ossidinge; Victoria. **Nigeria:** Lagos; Old Calabar. **Togoland:** Misahöhe. **Ghana:** Anecober River. **Sierra Leone:** (*fide* Aylmer). **French Guinea:** Beyla.

*Range.* Belgian Congo northwest to French Guinea.

## Genus PHILOTHAMNUS Smith[48]

1840. *Philothamnus* A. Smith, Ill. Zool. S. Africa, Rept., footnote to text for pl. lix. Type by monotypy: *Dendrophis* (*Philothamnus*) *semivariegata* A. Smith.

1857. *Chlorophis* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 52. Type by monotypy: *C. heterodermus* Hallowell.

1866a. *Herpetaethiops* Günther, Ann. Mag. Nat. Hist., (3) **18**, p. 27. Type by monotypy: *H. bellii* Günther = *C. heterodermus* Hallowell.

1868. *Chlorophis* Theobald, Cat. Rept. Asiatic Soc. Mus., p. 49. Type by monotypy: *C. oldhami* Theobald = *Ahaetulla hoplogaster* Günther.

1895h. *Oligolepis* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 171. Type by monotypy: *O. macrops* Boulenger.

In earlier days members of this genus were referred to *Coluber* (in its Linnaean sense), or to the Asiatic genera *Ahaetulla* (or its synonyms *Dendrophis* and *Leptophis*) and *Cyclophis* (now a synonym for *Opheodrys*).

*Definition.* Maxillary teeth 20-40, subequal or posterior longest; mandibular teeth subequal. Head more or less elongate, distinct from neck; eye moderately large, with round pupil; nasal divided; a loreal (rarely fused with prefrontal); a preocular (rarely divided). Body cylindrical, elongate; scales smooth, with apical pits, in 11-15 rows, narrow and disposed obliquely on anterior part of body; ventrals rounded or more or less sharply keeled on either side, usually a notch corresponding to the keel in

[48] The revision of this genus and those preceding it were ready for press when I received a copy of Laurent's monumental work on Central African herpetology (1956). With the preceding genera I was able to incorporate most new observations, but in the case of *Philothamnus* Laurent's wealth of material enabled him to observe aberrations almost as numerous as my own. For these and his comments on them, Laurent's paper should be consulted.

strongly keeled species. Tail long; subcaudals paired, not or but rarely keeled and notched (subgenus *Chlorophis*), or else normally keeled and notched (subgenus *Philothamnus*).

*Range.* All Africa (where suitable forest, savanna, bush or swamp conditions occur) south of 16° N., except in the extreme southwest (see distributional chart for the range of individual species).

*Remarks.* Proportions which are subject to change with growth (*vide* Parker: 1949) or other factors, do not provide a stable foundation for taxonomic purposes. Nevertheless, I have painstakingly examined all the available material for them — except the very lengthy series of *i. battersbyi*, *i. irregularis* and *s. semivariegatus*. In those forms where an abundance of material was available for study, a wide variation in scale proportions was noted. Naturally the bulk of the species fall within a mean, a few overlapping from this mean to extremes on one side or the other. A summary of these characters that are more or less common to all species in this rather homogeneous assemblage, follows:

Rostral broader than deep, the portion visible from above measuring about one quarter (*natalensis* and *semivariegatus* subspp.) or a third to a half (almost all species) to two-fifths (*heterodermus*, *hoplogaster* and *i. irregularis*) its distance from the frontal; internasals slightly shorter than, or as long as, the prefrontals (both conditions in all species where a good series was available, and in *hoplogaster* even longer than the prefrontal); frontal one-and-a-third to one-and-a-half times as long as broad (in most of the species) but one-and-a-quarter to twice as long as broad in *heterodermus*, as long as, or longer than, its distance from the end of the snout (both conditions in every form except *i. ornatus*, *s. girardi* and *s. thomensis* of which material is lacking or meagre), shorter than (in all species except *s. girardi* and *s. thomensis*) or as long as (in 7 forms) the parietals; loreal (rarely fused with a prefrontal in *hoplogaster*, *i. battersbyi* and *natalensis*) varies from one-and-a-quarter to twice as long as deep (in *i. battersbyi* and *heterolepidotus*) to one-and-two-thirds to three times as long as deep (in *s. semivariegatus*); a useful summary of loreal/nasal ratio in all British Museum material of *semivariegatus* was recently

published by Parker (1949a, pp. 58-61) but the loreals (and subcaudals) of our Pemba snakes are well within the range of variation exhibited by mainland specimens; the preocular is in contact with, or separated from, the frontal (both conditions in all ten adequately represented forms); the anterior sublinguals are shorter than, subequal to, or longer than, the posterior (all three conditions in *heterodermus*, only the two former in most of the others).

Assuming that the evolution of these snakes has proceeded from the generalized *macrops* to the specialized *semivariegatus*, we observe an increase in temporals, midbody scale rows, ventrals and subcaudals is taking place. The development of lateral keels (though these may be present or absent in several of the swamp or bush-dwelling intermediate forms) on both ventrals and subcaudals attains its highest perfection in *s. semivariegatus*, the species best adapted to an arboreal life and enjoying the widest distribution of any member of the genus. Yet it seems strange that the slight sexual difference in subcaudal counts that may be noted in *macrops* and its allies is lost in s. *semivariegatus*. If, on the other hand, we postulate that the widespread *semivariegatus* is the oldest species and developed when Africa supported more forest than is the case today, then it might be argued that the loss of keels is correlated with the departure to a more terrestrial existence in which frogs, instead of lizards, form the principal object of pursuit.

Due to the difficulty of deciding whether or not the subcaudals of an occasional *P. i. irregularis* are keeled, or those of a *s. nitidus* not, I (1951a:p. 189) suggested *Chlorophis* be regarded as of subgeneric status only, a view that has found general, though not universal, acceptance among my colleagues.

Either as *Ahaetulla*, *Chlorophis* and/or *Philothamnus*, quite a number of keys or summaries to this genus have been published by Günther (1863, pp. 283-287), Bocage (1882c, pp. 1-19), Boulenger (1894a, pp. 91-102), Günther (1895, pp. 527-528), Schmidt (1923, pp. 73-79), Hecht (1929, pp. 329-335), and Loveridge (1951c, pp. 1-12). The key now offered is the last one brought up to date. It was principally based on the abundant material in the Museum of Comparative Zoology, augmented by extensive loans of critical material from more than half-a-dozen

museums. The types of thirteen species or their synonyms, preserved in the British Museum, have been studied in detail. Unfortunately the more we know of variation in these reptiles, the more difficult it becomes to devise a clear, yet comprehensive, key. Aberrations from the normal are sufficiently frequent as to make it wise to use the key with the utmost caution, and take into consideration the ranges as set forth in the chart.

It is as well to admit that I am not satisfied about a few species and races (*i. irregularis, heterolepidotus, s. nitidus, s. dorsalis* and *s. semivaricgatus*) whose ventral and subcaudal counts (also, in some instances, geographical ranges) overlap. The only way to be confident that no misidentifications in the literature have been accepted, would be to borrow all the specimens listed in the literature from all the museums concerned — a somewhat overwhelming undertaking which I should like to see done.

## *Key to the Species*[49]

1. Subcaudals rounded or angular, occasionally faintly notched, but not so angular as to be called keeled; in most species less than 130 pairs of subcaudals[50] ..... 2 (*Chlorophis*)

   Subcaudals sharply angular (not always so in *s. dorsalis*), keeled and notched like the ventrals; usually more than 130 pairs of subcaudals. ..... 10 (*Philothamnus*)

2. Midbody scale-rows 13, very rarely 11 ..... 3

   Midbody scale-rows 15, very rarely 13 ..... 4

3. Anal divided, very rarely entire; usually 2 labials entering orbit; temporals 1 + 1 or 1 + 2, very rarely 2 + 2; range: montane forests of eastern Tanganyika Territory and a rice swamp in Zanzibar .... ..... *macrops* (p. 58)

[49] Not *every* individual snake will respond to this key as exceptions to the normal are numerous in this genus. Mistakes in identification may be avoided by taking into account the range, consulting the variational and distributional charts on pp. 55-57, and checking with the full description given under each species.

Before using this key the material should be sexed by making a longitudinal slit on the underside of the base of the tail with a razor blade. If a ♂, the elongate hemipenes will be found lying side by side; if a ♀, only minor blood vessels and muscular tissue will be present.

[50] Prior to counting the subcaudals it is equally important to ascertain if the tail tapers *gradually* to a fine point. The presence of a conical point is not necessarily proof that the tail is intact, for, when lost early in life, the terminal point may be regenerated.

Anal entire; usually 3 labials entering the orbit; temporals 2 + 2, very rarely 1 + 2, 2 + 1, 2 + 3 or 3 + 2; range: virgin forests of western Kenya (Kaimosi), west to the Cameroons and Fernando Po. Also French Guinea ..... *h. carinatus* (p. 60)

4. Anal entire; subcaudals 79-99; temporals usually 2 + 2, occasionally 1 + 1, 1 + 2, 1 + 3, 2 + 1 or 2 + 3 ..... 5
Anal divided, very rarely entire in *i. battersbyi*, *i. irregularis* and *heterolepidotus*); subcaudals 73-134 ..... 6

5. Ventrals 142-164; adult ♀♀ attain 862 mm.; range: virgin forests of Angola, north and west to Portuguese Guinea ..... *h. heterodermus* (p. 63)
Ventrals 174-181; adult ♀♀ attain 962 mm.; range: virgin forests of southwest Uganda, Belgian Ruanda and adjacent Belgian Congo south to Mpala ..... *h. ruandae* (p. 68)

6. Usually 2, though occasionally 3, labials entering orbit; range: eastern half of Africa ..... 7
Usually 3, though occasionally 2, labials entering orbit; range: western Africa, penetrating the East only in the Nyasa-Zambezi region 8

7. Subcaudals in ♀♀ 73-98, in ♂♂ 87-106; range: eastern Africa south of the Usambara Mountains in Tanganyika Territory, south through Mozambique and the Rhodesias to Port Elizabeth and Durban, South Africa ..... *hoplogaster* (p. 70)
Subcaudals in ♀♀ 90-111, in ♂♂ 100-120; range: eastern Africa in the Usambara Mountains, north through Kenya to Ethiopia, west to the Nile in the Sudan and Uganda (where it meets with the typical form), south around Lake Victoria, Tanganyika Territory ..... *i. battersbyi* (p. 76)
Subcaudals in ♀♀ 114-122, in ♂♂ 120-128; range: Transvaal, south to Natal and eastern areas of Cape Province, South Africa ..... *natalensis* (p. 98)

8. A broad brown dorsal stripe[51] on back and tail; range: Angola, east to Northern Rhodesia (Lealui) ..... *i. ornatus* (p. 82)
No such distinct dorsal stripe (unless occurring occasionally as a recessive character) ..... 9

[51] Possibly this stripe is not diagnostic in which event the name *ornatus* might be applied to all southwestern *irregularis* which have much lower scale-counts than those in the extreme northwest of Africa.

9. Subcaudals in ♀♀[52] 97-116, in ♂♂ 103-126; build moderately slender, more so in ♂♂ than in ♀♀; range: Senegal due east to Metemma on the White Nile, south down the Rift Valley (Lakes Victoria, Tanganyika, and both sides of Nyasa) following the Zambezi to the East Coast; south of the Zambezi it occurs from Southern Rhodesia west to Damaraland, north and west to Senegal ..... *i. irregularis* (p. 85)

Subcaudals in ♀♀ 109-126, in ♂♂ 115-134; build excessively slender, except in gravid ♀♀, but head noticeably narrower than in *i. irregularis;* range: Khartoum on the White Nile, southeast to mouth of Rovuma River, Tanganyika Territory (? Mozambique also), west to Angola, northwest to Togo, east to the Nile ..... *heterolepidotus* (p. 100)

10. Midbody scale-rows 13; range: Annobon Island, Gulf of Guinea ..... *s. girardi* (p. 124)

Midbody scale-rows 15, rarely 13 ..... 11

11. Ventrals 153-217; subcaudals 115-161 ..... 12

Ventrals 200-220; subcaudals 156-175; range: Sao Thomé Island, Gulf of Guinea ..... *s. thomensis* (p. 125)

12. Snout usually pale brown; temporals usually 1 + 1, very rarely 2 + 2 or 2 + 3; range: Angola, north to Cabinda and possibly Ogowe River, French Congo ..... *s. dorsalis* (p. 121)

Snout not distinctively colored; temporals usually 1 + 2 or 2 + 2 ..13

13. Ventrals 153-162; temporals usually 1 + 1 or 1 + 2, sometimes 2 + 2; range: virgin forests of French Congo, north through Cameroons, west to Ghana[53] ..... *s. nitidus* (p. 119)

Ventrals 164-217; temporals usually 2 + 2, sometimes 1 + 1, 1 + 2, 2 + 1 or 2 + 3; range: Eritrea south to Natal and adjacent areas of Cape Province, northwest to Gambia, i.e. all Africa south of 16° N. except Cape Peninsula, etc. ..... *s. semivariegatus* (p. 105)

[52] This is my lowest count for an intact tail, figures in the eighties occur in the literature, chiefly from Angola. If intact, possibly these should be referred to *i. ornatus* and less stress on dorsal band.

[53] This is a restricted concept of *nitidus* to that previously published by me (1951c, p. 5), and which was apparently followed by Laurent (1956). See footnote to *P. s. nitidus* on this matter.

## STATISTICAL DATA FOR THE SPECIES OF *PHILOTHAMNUS*

(Parentheses are employed to indicate abnormal variations; others are dealt with in footnotes to the specific descriptions)

| Species | Midbody scale-rows | Male ventrals | Female ventrals | Anal single divided | Female caudals (paired) | Male caudals (paired) |
|---|---|---|---|---|---|---|
| *macrops* | (11)13 | 135-146 | 135-148 | (S) D | 74-88[54] | 84-97 |
| *h. carinatus* | 13 | 141-157 | 145-167 | S | 72-86 | 78-91 |
| *h. heterodermus* | 15 | 142-160 | 152-164 | S (D) | 79-97 | 79-94 |
| *h. ruandae* | 15 | 174 | 175-181 | S | 82-93 | 99 |
| *hoplogaster* | (13)15 | 141-160 | 143-164 | D | 73-98 | 87-106 |
| *i. battersbyi* | 15 | 147-169 | 153-177 | (S) D | 90-111[55] | 100-120[55] |
| *i. ornatus* | 15 | 150-160 | 160-166 | D | 85-99 | 102-106 |
| *i. irregularis* | 15 | 150-179 | 153-183 | (S) D | 87-119[56] | 103-127 |
| *natalensis* | 15 | 150-165 | 151-168 | (S) D | 114-122 | 120-128 |
| *heterolepidotus* | 15 | 164-193[57] | 169-193 | (S) D | 109-126 | 115-134 |
| *s. semivariegatus* | (13)15 | 164-217 | 164-200 | D | 126-161 | 127-160 |
| *s. nitidus* | 15 | 153-162 | 154-164 | D | 133-151 | 136-153 |
| *s. dorsalis* | 15 | 167-190 | 172-180 | D | 115-137 | 128-143 |
| *s. girardi* | 13 | 185-197 | | D | 143-160 | |
| *s. thomensis* | 15 | 200-220 | | D | 156-175 | |

[54] A re-examination of the Nchingidi ♀ (M.C.Z. 48272) reported as having 69 subcaudals, suggests the tip was regenerated early in life.

[55] Uthmöller's (1938) counts of 118 for a ♀, and 123 for a ♂, require verification; unfortunately the specimens were destroyed during World War II.

[56] 87-93 in Dundo ♀♀ (*fide* Laurent :1950) which may possibl ybe referable to *i. ornatus* in a new sense; 97 was encountered in an Mtimbuka ♀ (M.C.Z. 51115) and a Mushongero ♀ (M.C.Z. 48288). Boulenger (1849a) gives up to 133 for West African snakes, but I suspect some of these may be *heterolepidotus*.

[57] With a variational range in ♂ ventrals of 30, it might be supposed that two races are involved; actually both extremes come from Niangara.

| Geographical Distribution of the African Genus *Philothamnus* | *macrops* | *h. carinatus* | *h. heterodermus* | *h. ruandae* | *hoplogaster* | *i. battersbyi* | *i. ornatus* | *i. irregularis* | *natalensis* | *heterolepidotus* | *s. girardi* | *s. thomensis* | *s. dorsalis* | *s. nitidus* | *s. semivariegatus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sudan | — | — | — | — | — | * | — | * | — | * | — | — | — | — | * |
| Eritrea | — | — | — | — | — | — | — | — | — | — | — | — | — | — | * |
| Ethiopia | — | — | — | — | — | * | — | — | — | — | — | — | — | — | — |
| British Somaliland | — | — | — | — | — | — | — | — | — | — | — | — | — | — | * |
| Somalia | — | — | — | — | — | * | — | — | — | — | — | — | — | — | * |
| Uganda Protectorate | — | * | — | * | — | * | — | * | — | * | — | — | — | — | * |
| Kenya Colony | — | * | — | — | — | * | — | — | — | * | — | — | — | — | * |
| Tanganyika Territory | * | — | — | — | * | * | — | * | — | * | — | — | — | — | * |
| Pemba Island | — | — | — | — | — | — | — | — | — | — | — | — | — | — | * |
| Zanzibar Island | * | — | — | — | — | — | — | — | — | — | — | — | — | — | * |
| Mafia Island | — | — | — | — | * | — | — | — | — | — | — | — | — | — | * |
| Mozambique | — | — | — | — | * | — | — | * | — | ? | — | — | — | — | * |
| Nyasaland Protectorate | — | — | — | — | * | — | — | * | — | — | — | — | — | — | * |
| Northern Rhodesia | — | — | ? | — | * | — | ? | * | — | — | — | — | — | — | * |
| Southern Rhodesia | — | — | — | — | * | — | — | * | — | — | — | — | — | — | * |
| Bechuanaland Protectorate | — | — | — | — | — | — | — | * | — | — | — | — | — | — | * |
| Transvaal, South Africa | — | — | — | — | * | — | — | — | * | — | — | — | — | — | * |
| Natal, South Africa | — | — | — | — | * | — | — | — | * | — | — | — | — | — | * |
| Orange River, South Africa | — | — | — | — | * | — | — | — | — | — | — | — | — | — | — |
| Cape Province, South Africa | — | — | — | — | * | — | — | — | * | — | — | — | — | — | * |
| South-West Africa | — | — | — | — | ? | — | — | * | — | — | — | — | — | — | * |
| Angola | — | — | * | — | — | — | * | * | — | * | — | — | * | — | * |
| Cabinda | — | * | * | — | — | — | — | * | — | * | — | — | * | — | — |

| Geographical Distribution of the African Genus *Philothamnus* | *macrops* | *h. carinatus* | *h. heterodermus* | *h. ruandae* | *hoplogaster* | *i. battersbyi* | *i. ornatus* | *i. irregularis* | *natalensis* | *heterolepidotus* | *s. girandi* | *s. thomensis* | *s. dorsalis* | *s. nitidus* | *s. semivariegatus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Belgian Congo | — | * | * | * | — | — | — | * | — | * | — | — | * | * | * |
| Belgian Ruanda-Urundi | — | — | * | * | — | — | — | * | — | * | — | — | — | — | — |
| French Congo | — | * | — | — | — | — | — | * | — | — | — | — | — | — | — |
| French Equatorial Africa | — | — | * | — | — | — | — | * | — | — | — | — | — | — | — |
| Annobon Island | — | — | — | — | — | — | — | — | — | — | * | — | — | — | — |
| Sao Thomé Island | — | — | — | — | — | — | — | * | — | — | — | * | — | — | — |
| Fernando Po Island | — | * | * | — | — | — | — | — | — | — | — | — | — | — | * |
| British Cameroon | — | * | * | — | — | — | — | * | — | * | — | — | — | * | — |
| French Cameroon | — | * | * | — | — | — | — | * | — | * | — | — | — | * | — |
| Nigeria | — | — | * | — | — | — | — | * | — | * | — | — | — | * | * |
| Dahomey | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Togo | — | — | * | — | — | — | — | * | — | * | — | — | — | * | * |
| Ghana | — | — | * | — | — | — | — | * | — | — | — | — | — | * | * |
| Ivory Coast | — | * | — | — | — | — | — | * | — | — | — | — | — | — | — |
| Liberia | — | — | * | — | — | — | — | * | — | — | — | — | — | — | * |
| Sierra Leone | — | — | * | — | — | — | — | * | — | — | — | — | — | — | — |
| French Guinea | — | — | * | — | — | — | — | * | — | — | — | — | — | — | * |
| Portuguese Guinea | — | — | * | — | — | — | — | * | — | — | — | — | — | — | * |
| Gambia | — | — | — | — | — | — | — | * | — | — | — | — | — | — | * |
| French West Africa | — | — | — | — | — | — | — | * | — | — | — | — | — | — | * |

### Philothamnus macrops (Boulenger)

1895b. *Chlorophis neglectus* Werner (not Peters), p. 193.
1895h. *Oligolepis macrops* Boulenger, Ann. Mag. Nat. Hist., (6) **16**, p. 171: Usambara Mountains, Tanganyika Territory.
1896d. Boulenger, p. 644.
1896. Tornier, p. 78.
1897. Tornier, p. 78 (reprinted).
1897b. Tornier, p. 65.
1908. *Chlorophis macrops* Sternfeld, p. 95.
1910a. Sternfeld, p. 19.
1911b. Sternfeld, p. 442.
1913b. Werner, p. 717.
1915c. Boulenger, p. 623.
1924b. Loveridge, p. 5.
1928c. Barbour & Loveridge, p. 116.
1929. Hecht, p. 330.
1929a. Werner, p. 100.
1934c. Mertens, p. 157.
1937f. Loveridge, p. 502.
1941a. Uthmöller, p. 40.
1942e. Loveridge, p. 270.
1947. Pakenham, p. 140.
1951c. Loveridge, pp. 3, 6.

*Common Names.* Usambara Green-Snake (Loveridge); nyoka ya mani (Sambaa:Loveridge).

*Description.* Preoculars 1, rarely 2; postoculars 2; temporals 1 + 1, 1 + 2 (or 2 + 2,[58] *fide* Sternfeld); upper labials 8, occasionally 9, the fourth and fifth (or fourth, fifth and sixth,[58] *fide* Sternfeld) or fifth and sixth entering the orbit; lower labials 8-12, the first 4, 5 or 6 in contact with the anterior sublinguals. Midbody scale-rows 13, rarely 11; ventrals 135-148[59] (♂♂ 135-146; ♀♀ 135-148); anal divided, rarely entire (M.C.Z. 23236 and some Zanzibar snakes only); subcaudals 74-97 (♀♀ 74-88; ♂♂ 84-97).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

[58] If these two aberrations were on the same snake, one wonders if a young *Philothamnus s. semivariegatus* might not have been included in Sternfeld's long series; impossible if he included all scale-counts.

[59] 148 in the ♀ holotype, confirmed by me, though I find 81, *not* 75 subcaudals.

*Color.* Above, green or bronzy green to olive or brown, the upper lip white; sometimes as many as 42 irregular light cross-bars formed by scales with a light yellow or green, black-edged, basal spot turning to light blue on flanks. Below, chin and throat white; rest of under surface pale green, yellowish green, or bluish-white, uniform, or each ventral shield with a lateral dull red blotch, or laterally bordered with black, the free edge tinged with bluish-gray.

*Size.* Length of ♂ (M.C.Z. 23236) 810 (560 + 250 )mm.; of a ♀ (M.C.Z. 23239) 950 (690 + 260) mm.; the unsexed juvenile holotype ♀ (Brit. Mus.) now measures 222 (165 + 57) mm., the youngest topotype ♂ (M.C.Z. 23246) 200 (130 + 70) mm.

*Remarks.* It was by the inclusion of a couple of the then undescribed *P. i. battersbyi* in their series of *macrops* from Amani, that Barbour & Loveridge (1928c) unduly increased the range of ventrals and subcaudals for that species. These two green snakes may be distinguished by *macrops* possessing fewer ventrals, i.e. 135-148 (147-177 in *battersbyi*), fewer subcaudals by sexes, i.e. 69-88 in ♀ ♀ (90-111 in ♀ ♀ *batterysbyi*), 84-97 in ♂ ♂ (100-120 in ♂ ♂ *battersbyi*), and 13 (instead of 15) mid-body scale rows. In this reduction of scale rows *macrops* parallels the situation of two other Amani forest-edge snakes which have lowland representatives: — *Natriciteres o. uluguruensis* (17 scales) *N. o. olivacea* (19 scales), *Crotaphopeltis h. tornieri* (17 scales), *C. h. hotamboeia* (19 or 21).

*Sexual dimorphism.* In ♀ ♀ the subcaudals range from 69 to 88.
In ♂ ♂ the subcaudals range from 84 to 97.

*Breeding.*

On November 19, at Amani, a ♀ held 5 eggs of 29 x 11 mm.
" 20, " " " 6 " 36 x 15 mm.
" 22, " " " 14 " 30 x 12 mm.
" 24, " " " 3 " 34 x 10 mm.

*Diet.* A chamaeleon (*Brookesia brevicaudata*); tail of a skink; and a frog (*Arthrolepis s. whytii*) were recovered from stomachs, but those of 15 other snakes taken at Amani during November were empty!

*Habitat.* In bushes fringing the forest and along the borders of nearby streams. Reported from a rice field in Zanzibar by Pakenham.

*Localities.* **Tanganyika Territory:** Rondo Plateau—*Nchingidi; Tanga; *Usambara Mountains—*Amani; Nguelo. **Zanzibar Island:** Kinuni, Moshi.

*Range.* Coastal Tanganyika Territory and, probably introduced by human agency, the adjacent island of Zanzibar.

### Philothamnus heterodermus carinatus (Andersson)

1897b. *Chlorophis heterodermus* Mocquard (not Hallowell), p. 12.
1897b. Werner, p. 403.
1933m. Witte (part), p. 89 ("Dika" should read Arebi).
1901. *Chlorophis carinatus* Andersson, Svenska Vetensk.-Akad. Handl., **27**, No. 5, p. 9: Mpanja, British Cameroon.
1908a. Sternfeld, pp. 407, 425.
1909b. Sternfeld, p. 15.
1910. Müller, p. 601.
1911. Lampe, p. 193.
1915a. Boulenger, p. 205.
1916. Andersson, p. 30.
1917. Sternfeld, p. 470.
1919a. Boulenger, p. 282.
1919g. Boulenger, p. 23.
1923. Schmidt, p. 74.
1927d. Witte, p. 323.
1929. Hecht, p. 331.
1929a. Werner, p. 100.
1933m. Witte, p. 80.
1934a. Schwetz, p. 380.
1936h. Loveridge, p. 28.
1936j. Loveridge, p. 243.
1936. Pitman, p. 274, pl. v, fig. 1; pl. E, fig. 4.
1937f. Loveridge, p. 502.
1938a. Pitman, p. 304.
1938b. Pitman, pp. 39, 87, 88, 295, 304-5, pls. (as in 1936).
1940. Bogert, p. 51.
1941. Mertens p. 278.
1941. Witte, p. 199.
1942e. Loveridge, p. 270.
1951. Monard, p. 150.
1951c. *Philothamnus heterodermus carinatus* Loveridge, pp. 3, 6.
1953. Witte, p. 193, fig. 55.
1954. Angel, Guibé, Lamotte & Roy, p. 392.
1954d. Laurent, pp. 296, 297.
1954b. Villiers, p. 1240.

*Common Names.* Thirteen-scaled Green-Snake (Loveridge); *kangasira* (Gishu:Loveridge); *lushangabanyeri* (Lega:Loveridge); *mukangaceni* (Kiga:Pitman).

*Description.* Preocular 1; postoculars 2, rarely 1, 3, or 4; temporals 2 + 2, rarely 1 + 2, 2 + 1, 2 + 3, or 3 + 2; upper labials 8-10, the fourth, fifth and sixth; rarely third, fourth and fifth; the fourth and fifth only; the fourth fifth, sixth and seventh; or fifth, sixth and seventh, entering the orbit; lower labials 8-11, the first 4, 5 or 6 in contact with the anterior sublinguals.

Midbody scale-rows 13; ventrals 141-167 (♂♂ 141-157; ♀♀ 145-167); anal entire; subcaudals 72-91 (♀♀ 72-86; ♂♂ 78-91).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above, green or olive; young with more or less distinct dark crossbars that tend to disappear with age; vertebral scales baso-laterally edged with pale blue. Below, chin white; throat yellowish; body and tail yellowish green to pale green.

In alcohol indistinguishable from the coloring of *P. hoplogaster* which was abundant at Sipi. Fortunately, I recorded the coloring of a freshly killed Sipi ♂ *carinatus* in the field, being struck by its difference from *hoplogaster*.

Above, dark olive with 104 deep-black, irregular crossbands between head and anus; on the tail these are represented by black flecks; the olive scales between the crossbands are edged with pale blue on the anterior two-thirds of the body; upper lip brownish olive anteriorly, white below the eye shading off into olive posteriorly. Below, throat pure white, anterior ventrals tinged with yellow, remainder of the under surface dark green with its anterior third heavily suffused with yellow; on the anterior two-thirds edged with yellow laterally, on the posterior third with bluish white, on the tail with dusky.

Center of the eye black, surrounded by a light area, then by a fine orange line, then by an olivaceous area flecked with black; outermost ring, black.

*Size.* Largest ♂ (M.C.Z. 42907), 721 (540 + 181) mm., from Bondo; a ♀ cotype (No. 1974), 815 (600 + 215) mm.; the youngest, a ♂ (M.C.Z. 40483), 408 (303 + 105) mm., is from Kaimosi.

*Remarks.* The recent (1954) discovery of *P. h. carinatus* with *P. h. heterodermus* in French Guinea, makes it extremely doubtful whether *carinatus* should be recognized as separable from *heterodermus*, its sole distinguishing feature being 13 midbody scale-rows. I retain it tentatively solely in the hope that further light may be shed on the incidence and range of *carinatus*.

*P. h. heterodermus* is present in 6 of the 9 countries from which *h. carinatus* has been recorded, but until its recent discovery on Mt. Nimba *carinatus* was unknown from west of the Cameroons, whereas typical *heterodermus* ranges all the way to Sierra Leone. Both forms occur together at Metet (M.C.Z. material), and have been recorded as doing so at Johann Albrechtshöhe; Ebolowa; Lonji; Molundu and Mukonje Farm, in the Cameroons (Sternfeld:1908a); both from Dika[60]; Medje; Stanleyville and Temvo, in the Belgian Congo (Witte:1933m etc.).

On the other hand one might says that *P. h. carinatus* is the Central African representative of the eastern forest *macrops*, seemingly an offshoot now separated by 450 miles. These are the only two members of the subgenus *Chlorophis* that regularly have 13 midbody scale-rows. See also comments by Laurent (1956) received after the above was written.

*Dentition.* In describing *carinatus* Andersson reported it as having "about 40" maxillary teeth. Bogert (1940) found 39, 41 and 42, of which the posterior 4 or 5 were larger and stouter than the rest. Dealing with Congo specimens, Bogert emphasizes the close affinities with *heterodermus*, not only in dentition, lepidosis, color and habitus, but also in hemipeneal characters.

*Hemipenis.* Not bifurcate; sulcus spermaticus undivided; basal spines well developed and merging distally into reticulate calyces which grade into numerous flattened papillae towards the tip, which extends to the sixth or seventh caudal (Bogert etc.).

*Sexual dimorphism.* A scarcely appreciable tendency for ♂♂ to average fewer ventrals and more subcaudals than ♀♀.

*Diet.* A frog (Sternfeld:1910).

*Enemies.* One recovered from the digestive tract of a vine-snake (*Thelotornis k. kirtlandii*) from whose mouth 30 mm. of the green snake's tail still protruded (Bogert).

[60] Both Dika specimens examined by me.

*Habitat.* Essentially a rain-forest form, but at Avakubi a *carinatus* fell from the thatch on to the collector's table (Schmidt).

*Localities.* **Uganda:** *Budongo Forest; Kayonza Forest, Kigezi (*fide* Pitman); *Sipi Forest, Mount Elgon. **Kenya Colony:** *Kaimosi. **Cabinda. Belgian Congo:** *Arebi; Avakubi; Babonde s. of Medje; Bafwasende; *Bambesa, Uele; Batama; Beni; Bunyakiri; *Buta; [Dika: in error]; Eala; Faradje; *Ibembo, Uele; *Idjwi Island—Upper Mulinga River; Ituri; Kande River; Kansenia; Kasai; Kaswabilenga; Katanga; *Kulu River; Kunungu; Lissinu; Lukawe River; Lukolela; Lusema; Maganga Bay; Manda; Manguretshipa; Medje (as Madié); Mombaka; *Mpala, Lualaba; *Mpesi-Ukesi, Lower Congo; Munoi; Nala; Niapu; *Panga, Aruwimi River; Shabunda region; *Stanleyville; Temvo; *Yangambi, Stanleyville; Walikale; *Zambi, Ubangi; *Zobia, Uele. **French Congo:** Lambarene (as *heterodermus*). **Fernando Po:** Bokoko-Garcia. **French Cameroon:** Dibongo; Ebolowa; Longji; *Metet; Molundu; Mukonje Farm. **British Cameroon:** Barombi; Bibundi; Buea; Camp; Isongo; Johann Albrechtshöhe; Mapanga (type locality). **French Guinea:** Mt. Nimba—Gouela; Nion.

*Range.* Western Kenya Colony, west through the Belgian Congo to Fernando Po. Also French Guinea.

### Philothamnus heterodermus heterodermus (Hallowell)

1857. *Chlorophis heterodermus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 54: Gabon = French Congo.
1860. Cope, p. 559.
1884a. Rochebrune, p. 173 (not used).
1894a. Boulenger, pp. 97, 358.
1896d. Boulenger, p. 631.
1897. Sjöstedt, p. 35.
1898. Boettger, p. 58.
1898a. Werner, p. 209.
1899a. Werner, p. 137.
1900b. Boulenger, p. 452.
1902a. Werner, pp. 338, 344.
1906i. Boulenger, p. 213.
1908a. Sternfeld, pp. 407, 425.
1908b. Sternfeld, pp. 214, 230.

1909a. Sternfeld, p. 14, fig. 20.
1909b. Sternfeld, p. 15, fig. 15.
1909d. Werner, p. 247.
1910. Müller, p. 601.
1912c. Boulenger, p. 470.
1917a. Phisalix, p. 334.
1917. Sternfeld, p. 469.
1919a. Boulenger, p. 282.
1921a. Chabanaud, p. 468.
1921b. Chabanaud, p. 524.
1922. Aylmer, pp. 15, 19.
1927d. Witte, p. 323.
1929. Hecht, p. 331.
1929a. Werner, p. 101.
1933f. Angel, p. 105, figs. 38-38a.
1933. Schouteden (part ?), p. 236.
1933j. Witte, p. 123.
1933m. Witte (part), p. 89.
1934c. Mertens, p. 169.
1934a. Schwetz, p. 380.
1936h. Loveridge (part), p. 29.
1936c. Parker, p. 125.
1938a. Pitman, pp. 294, 305, pl. xvii, fig. 3, pl. T, fig. 2.
1940. Bogert, p. 52.
1940a. Mertens p. 241.
1940b. Monard, p. 174.
1941. Witte (part), p. 198.
1945. Leeson, p. 1.
1948d. Cansdale, p. 45, photo.
1950. Leeson, pp. ix, 39, 40, 66, 133.
1950a. Villiers, p. 59.
1950b. Villiers, p. 80, figs. 94-95.
1951. Monard, p. 149.
1863c. *Ahaetulla heteroderma* Günther, p. 285.
1885. Müller, p. 683.
1866a. *Herpetaethiops Bellii* Günther, Ann. Mag. Nat. Hist., (3) **18**, p. 27, pl. vii, fig. B: Sierra Leone, i.e. Victoria, Sherbro Island, Sierra Leone.
1884a. Rochebrune, p. 171 (not used).
1875a. *Philothamnus heterodermus* Peters, p. 199.
1882c. Bocage, p. 18.
1888a. Boettger, p. 59.
1891b. Matschie, p. 615.

1893c. Matschie, p. 212.
1895a. Bocage, p. 89.
1882a. *Ahaetulla* sp. Müller, p. 149.
1885. Müller, p. 683.
1884b. *Philothalmus heterodonta* (*sic*) Sauvage, p. 201.
1893. *Philotamnus eterodermus* (*sic*) Prato, p. 11.
1916f. *Chlorophis heterodermus Pobeguini* Chabanaud, Bull. Mus. Hist. Nat. (Paris), **22**, p. 371, fig. 12: French Guinea.
1929. Hecht, p. 331.
1933f. Angel, p. 106.
1940b. Monard, p. 174.
1929. *Chlorophis cyaneus* Hecht, Zool. Anz., **81**, pp. 331, 334, figs. 1-2: Ajoshöhe, Nyong River, British Cameroon.
1951. Monard, p. 150.
1951c. *Philothamnus heterodermus heterodermus* Loveridge, pp. 3, 6.
1954. Angel; Guibé; Lamotte & Roy, p. 392.
1954b. Villiers, p. 1240.

Further citations of "*heterodermus*" will be found under *h. carinatus*.

*Common Names.* Emerald Green-Snake (Aylmer); Variable Tree-Snake (Cansdale); *boprakala* (Temne:Aylmer); *ndawundukali* (Mende:Aylmer); Pitman supplies the general Ganda and Kiga names for *Chlorophis*, but unless *h. carinatus* is a synonym it is questionable whether *h. heterodermus* occurs in Uganda.

*Description.* Preoculars 1, sometimes 2; postoculars 2, rarely 1 (*fide* Angel) or 3; temporals occasionally 1 + 1, 1 + 2, 1 + 3 (*fide* Müller) or 2 + 1, though normally 2 + 2 or 2 + 3; upper labials 8-10, the third, fourth and fifth[61]; fourth and fifth (type of *cyaneus*); fourth, fifth and sixth; fifth and sixth (type of *pobequini* on one side only); or fifth, sixth and seventh, entering the orbit; lower labials 9-11, the first 5, rarely 4,[62] in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 152-164 (♂ ♂ 142-160; ♀ ♀ 152-164); anal entire, rarely divided[63]; subcaudals 79-97 (♀ ♀ 80-97; ♂ ♂ 79-94).

[61] On right side of a Kumasi ♂ (M.C.Z. 53691), on whose left side is the more usual 9, with fourth, fifth and sixth entering.

[62] On left side of an Achimota ♂ (C.N.H.M.), on whose right side are the normal 10 labials, the first 5 of which are in contact with the anterior sublinguals (examined by A.L.).

[63] Divided in a Somanya ♂ (M.C.Z. 55212).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above blue-green or olive, the interstitial skin black; anterior part of back in young occasionally shows a longitudinal series of paired black spots that sometimes coalesce to form crossbars; some scales spotted with white, with or without a dark edge. Below, chin and throat yellowish cream; body and tail cream to pale or bluish green.

In life, writes Cansdale (letter of 23.ii.51), an Oda snake measuring 635 (465 + 170) was: Above, head dark olive brown; body olive brown with irregular dark crossbands and noticeably white between scales. Below, throat and body orange yellow gradually merging into dark slate posteriorly; tail uniformly dark slate. However, another Oda snake of 549 + 190 mm. (No. 183), as also a Kumasi specimen (No. 154), were recorded as "Black."

Such melanistic individuals, says Cansdale, might easily be mistaken for a small black cobra. In this connection it will be noted that the type of *bellii* was described as: Above, deep black. Below, deep black except for chin, throat and thirty anterior ventrals, which are whitish. I assumed that this was due to formalin preservation until I came across Dr. Harley's reference to a Ganta snake being purple with a green head (Bogert), and Cansdale's comments about a similarity to a small black cobra.

*Size.* Length of ♂ (type of *pobeguini* in P.M.) 780 (595 + 185) mm., but a comparison with the measurements of a ♀ suggests the tail tip is regenerated; consequently Chabanaud's count of 77 caudals is rejected. Length of ♀ (type of *bellii* in B.M. 46.1.10.27) 867 (650 + 217) mm., but surpassed by another ♀ (B.M. 36.8.1.669) of 886 (660 + 226) mm. from Congulu; the youngest, a ♀ (M.C.Z. 13230) from Metet, 344 (255 + 89) mm.

*Remarks. P. h. heterodermus* is probably an offshoot of *irregularis*, from normal specimens of which it differs in having fewer subcaudals (see chart on p. 55), a single anal, and usually 2 + 2 temporals — though both these last characters may occur occasionally in *irregularis.*

The possibility of a short-tailed western race occurring in Sierra Leone requires investigating; if recognizable, the name *bellii* would be available. Though normal *heterodermus* have been reported from Portuguese and French Guinea, *P. h. pobeguini* was based on a single specimen from the latter country. The type had only 2 upper labials entering the orbit, and a temporal arrangement of 2 + 1 on the right side, 1 (incompletely divided) + 1 on the left side. Monard has recorded a second specimen from Portuguese Guinea, having 9 upper labials, the fifth and sixth entering the orbit, and temporals 1 + 1. Two Cameroon snakes (M.C.Z. 7849; 13233) with the normal 9 upper labials, of which the fourth, fifth and sixth enter the orbit on one side of the head, have the *pobeguini* arrangement on the other side. Further discussion on the synonymy of this snake, and that of *cyaneus,* will be found in an earlier (1936h) paper by me.

*Dentition.* The type of *cyaneus* had 30-32 maxillary teeth (Hecht); there were 33 and 35 in two Cameroon *heterodermus* examined by Bogert (1940), who points out that this species apparently has 5 more maxillary teeth than *irregularis.* See also Leeson (1950).

*Anatomy.* The presence of parotids is discussed by Phisalix (1917a).

*Hemipenis.* Not bifurcate; sulcus spermaticus undivided; basal spines enlarged and followed by 2 or 3 flounces, merging distally into reticulate calyces which grade into numerous fine papillae towards the tip, which extends to the seventh caudal (Bogert).

*Sexual dimorphism.* Negligible, though probably some average differences could be demonstrated with more material.

*Breeding.* In June, at Dika, a ♀ held eggs measuring about 23 x 7 mm. (A.L.). In November, at Worawora, a ♀ held 5 eggs measuring about 35 x 10 mm.

*Diet.* A frog (Werner:1909d); feeds on lizards in Sierra Leone according to Aylmer (1922).

*Habitat.* Frequently found in gardens, according to Aylmer (1922), who may be confusing it with *i. irregularis.*

*Localities.* **Angola:** *Congulu. **Belgian Congo:** *Banana; Burunga; *Dika; Ganda-Sundi; Kai-Bumbi; Kamatembe: Kibumba; Kisala; *Kisantu; *Lufu; Lukula; *Makaia Ntete; Medje; Povo Nemlao; Rugari; *Stanleyville *Temvo* Tshumba. **French Equatorial Africa:** Fort Sibut; Gabon. **Fernando Po:** Bahia de Sao Carlos. **French Cameroon:** Bipindi; Bitye; Ebolowa; *Efulen; *Kribi; Longji; *Metet; Molundu; Mukonje Farm, Mundame; *Sakbayeme. **British Cameroon:** Ajoshöhe, Nyong River (type of *cyaneus*); Johann Albrechtshöhe; Buea; Tiko; Victoria. **Nigeria:** Lagos; Niger River; Oban District; Oil River. **Togo:** Adele (Bismarckburg); Misahöhe; *Worawora. **Ghana:** Accra; *Achimota; *Adjikpo; Ashanti; *Kumasi; Odumasi; *Somanya. **Ivory Coast:** Banco Reserve; Tonkui Mountain. **Liberia:** Ganta; *Suacoco. **Sierra Leone:** Freetown; Victoria, *Sherbro Island (type of *bellii*). **French Guinea:** Guelemata; Macenta; Nimba Mountain; Nion; Nzebela; Nzo; To Mountain. **Portuguese Guinea:** Catio; Madina Boe; Rio Cassine.

*Range.* Angola north and west to Portuguese Guinea (for Uganda, Ruanda, and some eastern Congo records, see *heterodermus ruandae*).

### Philothamnus heterodermus ruandae Loveridge

1933j. *Chlorophis heterodermus* Witte (not Hallowell), p. 123.
1933m. Witte (part), p. 89 (Birunga; Lulenga).
1936h. Loveridge (part), p. 29 (Lake Kivu).
1941. Witte (part), p. 198 (Kamatembe; Lake Kivu; Rugare).
1951e. *Philothamnus heterodermus ruandae* Loveridge, Inst. roy. Sci. nat. Belgique, Bull. **27**, No. 37, pp. 2, 7: ♀ ex Mulungu, Lake Kivu, Belgian Congo.
1953. Witte, p. 195.
1956. Laurent, p. 174, fig. 26, pl. xix, fig. 1.

*Common Name.* Ruanda Emerald-Green-Snake.

*Description.* Preoculars 1-2[64]; postoculars 2; temporals 1 + 2, 2 + 2 or 2 + 3; upper labials 8-10, the third, fourth and fifth; fourth, fifth and sixth; or fourth, fifth, sixth and seventh enter-

[64] Two on the left side of a Kayonza ♂ (C.N.H.M. 6975).

ing the orbit; lower labials 8-11, the first 4, 5 or 6 in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals[65] 165-181 (♂♂ 165-174; ♀♀ 175-180); anal entire; subcaudals 82-100 (♀♀ 82-93; ♂♂ 98-100).

*Color.* As in *P. h. carinatus*, with the snout and throat at least partially drab (Laurent).

*Size.* Total length of ♂ (C.N.H.M. 6975) 725 (515 + 210) mm.; largest ♀ (I.G. 16964) 962 (730 + 232) mm.; holotype ♀ (I.G. 15860) 912 (680 + 242) mm.

*Remarks.* From its nearest relatives (of which I have about 75 and 40 counts respectively, the 7 specimens of *ruandae* seen by me and an additional 20 or so listed by Laurent (1956), differ in their more numerous ventrals and larger size; characters best seen in a comparative table.

| Species | Mid-body scale-rows | Ventrals in ♂♂ | Ventrals in ♀♀ | Caudals in ♀♀ | Caudals in ♂♂ | Largest ♀ in mm. |
|---|---|---|---|---|---|---|
| *h. carinatus* | 13 | 141-157 | 145-167 | 72-86 | 78-91 | 815 (600 + 215) |
| *h. heterodermus* | 15 | 142-160 | 152-164 | 79-97 | 79-94 | 886 (660 + 266) |
| *h. ruandae* | 15 | 165-174 | [65]171-181 | 82-93 | 98-100 | 962 (730 + 232) |

*Sexual dimorphism.* In addition to the ventral and subcaudal counts tabulated above, Laurent finds the percentage of tail lengths into total lengths of 15 ♀♀ is 24 to 26.6%, while in 3 ♂♂ it is only 27.5 to 29%.

*Diet.* Frogs recovered from stomachs of *ruandae* by Laurent, have been identified as *Leptopelis karissimbiensis* (ex Alimbongo); *Schoutedenella* sp. (ex Kabilombo), and *Rana fuscigula* (ex Mount Kabobo).

*Localities.* **Uganda:** Impenetrable Forest, Kayonza, British Ruanda. **Belgian Ruanda-Urundi:** Bugarama; Kabobo; *Lake Kivu; *Lulenga; Mulungu; Nyongwe. **Belgian Congo** in Kivu region: Alimbongo; Burunga; Kabilombo; Kabumbe; Kamatembe; Kibumba; Rugare; Tshumba; Uvira; also allegedly from Mpala, Kanzenze, Lualaba District.[66]

[65] 164 in a Kabobo ♀ according to Laurent (1956) who considers it aberrant.

[66] See Laurent, whose paper is a major contribution to our knowledge of this form, for reasons why this locality is probably erroneous.

*Range.* Southwestern Uganda, west through Belgian Ruanda-Urundi to the Belgian Congo.

PHILOTHAMNUS HOPLOGASTER (Günther)

1863c. *Ahaetulla hoplogaster* Günther, Ann. Mag. Nat. Hist., (3) 11, pp. 284, 286: "Port Natal" i.e. Durban, Natal, South Africa.
1890. Boulenger, Fauna British India, Rept. & Batr., p. 305.
1866b. *Philothamnus neglectus* Peters, Monatsb. Akad. Wiss. Berlin, p. 890, footnote: "Prazo Boror" i.e. Boror, Mozambique.
1882a. Peters, p. 130, pl. xixA, fig. 2.
1893. Pfeffer (part), p. 84 (omit Usambara).
1896a. Bocage, p. 92.
1868. *Chlorophis Oldhami* Theobald, Cat. Rept. Asiatic Soc. Mus., p. 49: "Simla, India" (in error).
1876. *Cyclophis oldhami* Theobald, Rept. British India, p. 159.
1882c. *Philothamnus hoplogaster* Bocage, p. 17.
1887h. Boulenger (part), p. 176 (omit Wynberg and Damaraland).
1951e. Loveridge, pp. 4, 7.
1953. Loveridge, pp. 260, 318.
1894a. *Ahaetulla neglecta* Günther, 1893, pp. 618, 620.
1898. Johnston, p. 361a.
1894a. *Chlorophis hoplogaster* Boulenger (part), p. 93, pl. v, fig. 2 (omit Damaraland and Lake Victoria).
1898. Boettger, p. 58.
1898. Sclater, p. 99.
1898. Werner, 1896-7, p. 143.
1907j. Boulenger, p. 486.
1907c. Roux, p. 734.
1908b. Boulenger, p. 228.
1908. Gough, p. 24.
1910b. Boulenger (part), p. 507 (omit key, etc.).
1910a. Hewitt, p. 57.
1910a. Sternfeld (part), p. 18.
1912. FitzSimons, F. W. (part), pp. 86, 87, 92 (omit key).
1913. Boettger, p. 363.
1914a. Hewitt (part), pp. 242, 245, 246 (omit counts).
1915a. Boulenger (part), p. 205.
1915c. Boulenger (part), p. 622.
1929. Flower, p. 203.
1929. Hecht (part), p. 332.

1929a. Werner, p. 100.
1933h. Loveridge (part), p. 236 (omit Ukerewe Id.).
1934. Pitman, p. 294.
1935. Cott, p. 966.
1935. Power, p. 334.
1937e. Hewitt, p. 59, fig. 1.
1937f. Loveridge, pp. 489, 496, 503.
1939b. FitzSimons, V. F., p. 22.
1940. Bogert (part), p. 54 (omit Lukolela).
1950. Rose, pp. 271, 320, fig. 166 (photo); p. 314, fig. 8 (head).
1955. Rose, pp. 93, 97 (faulty key), fig. 43 (photo); p. 178, fig. 8 (head).
1894a. *Chlorophis neglectus* Boulenger (part), p. 94 (omit localities in Kenya and Tanganyika).
1896d. Boulenger (part), p. 631 (omit Witu).
1896. Peracca, p. 2.
1897. Tornier, p. 65.
1898. Tornier, p. 294.
1899a. Mocquard, p. 219.
1907a. Boulenger, p. 10.
1907. Lönnberg, p. 15.
1908b. Mocquard, p. 558.
1908c. Sternfeld, p. 246.
1910b. Boulenger (part), p. 507 (omit key).
1910. Peracca, p. 4.
1910a. Sternfeld (part), p. 18 (omit Kagera, etc.).
1912. FitzSimons, F. W. (part), pp. 86, 87 (omit key).
1912. Peracca, p. 5.
1913. Boettger, p. 345.
1913. Hewitt & Power, p. 162.
1915a. Boulenger (part), p. 205.
1915c. Boulenger (part), p. 623.
1915d. Boulenger (part), p. 648.
1928c. Barbour & Loveridge (part), p. 115 (omit Usambara localities).
1928. Cott, p. 953.
1928j. Loveridge, p. 74.
1929. Flower, p. 203 (omit range).
1929. Hecht (part), pp. 332, 333.
1929a. Werner (part), p. 100.
1933h. Loveridge, p. 237.
1934. Pitman, p. 294.
1935. Cott, p. 966.

1937a. Parker, p. 630.
1941. Moreau & Pakenham, p. 108.
1941. Themido, p. 16.
1942c. Loveridge, p. 271.
1943. Scortecci, p. 270.
1950. Ionides, p. 101.
1950. Rose, pp. 271, 320.
1955. Rose, pp. 93, 97 (faulty key).
1902b. *Chlorophis natalensis* Boulenger (not Smith), p. 17.
1910b. Boulenger (part), p. 507 (Kafue River record only).
1948a. FitzSimons, V. F., p. 73, pl. i, fig. 1.
1933m. *Philothamnus dorsalis* Witte (part, not Bocage), p. 89.

Further citations of "*hoplogaster*" and "*neglectus*" will be found under *macrops, i. battersbyi, i. ornatus, i. irregularis* and *heterolepidotos.*

*Common Names.* Southeastern Green-Snake (Loveridge); Green Water-Snake (FitzSimons); Leaf-Snake (Cott); *imbindipidni* (Nyakusa:Loveridge); *masamandimo* (Sena:Cott); *nalwinduwindu* (Misuku:Loveridge); *namalanga* (Makonde:Loveridge); *namasamba* (Nyanja, but not even generic); *nyaluwina* (Hehe:Loveridge); *nyoka amani* (Sambaa:Loveridge); *nyoka msipu* (Chewa; Ngoni:Loveridge).

*Description.* Preoculars 1, rarely 2; postoculars 2, rarely 3; temporals 1 + 1, rarely 1 + 0, 1 + 2, 2 + 1 or 2 + 2; upper labials 7-9, the fourth and fifth, rarely the third and fourth, the third, fourth and fifth, the fourth, fifth and sixth, or the fifth and sixth, entering the orbit; lower labials 9-11, rarely 13,[67] the first 4, 5, or 6 in contact with the anterior sublinguals. Mid-body scale-rows 15, very rarely 13 or 14[68]; ventrals 130[69] or 141-164 (♂♂ 141-160[70]; ♀♀ 143-164); anal divided; subcaudals 73-106 (♀♀ 73-98[71]; ♂♂ 87-106).

[67] Thirteen on one side only of a Nyange snake (M.C.Z. 23208).

[68] Thirteen on a Fort Johnston ♀; 14 on a Zomba ♀ (Loveridge:1953h).

[69] 130 on an aberrant Rungwe reptile recorded and verified by Bogert (1940:54); 141 is the lowest count for 30 ♂♂ in the Museum of Comparative Zoology.

[70] 161-163 (Laurent:1956) and 173 given by de Witte (1953:183) requires checking, as do his low subcaudal counts (♀♀ 59-88; ♂♂ 78-105) which may be due to inclusion of specimens with regenerated tail tips.

[71] 98 in a Mazoe snake (B.M. 02.2.12.87), and 91, *not* 93, in one ♀ cotype.

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above green, the interstitial skin black, uniform, or nape and anterior part of back with a longitudinal series of paired black, blue (at Ilolo), or brown (in life at Lake Rutamba) spots, that sometimes coalesce to form crossbars; some scales with a white basal spot. Below, pure white to very pale green.

Seven black crossbars on a young snake, found in a heap of debris beneath a mango tree at Mikindani, gave it some resemblance to a young night-adder (*Causus resimus*). F. W. FitzSimons (1912) remarks that where they occur together, green-snakes are apt to be mistaken for the young of the Green Mamba (*Dendroaspis angusticeps*).

*Size.* Length of cotype ♂ (Brit. Mus.), 650 (432 + 218[72]) mm. from Durban; exceeded by a ♂ (M.C.Z. 51101), 720 (500 + 220) mm. from the Misuku Mountains, and, if sex and determination are correct, one of 821 (638 + 183) mm. recorded by de Witte. Largest ♀ (B.M. 02.2.12.87), 945 (685 + 260) mm. from Mazoe (measured by me).

*Remarks. C. hoplogaster* of Boulenger (1894a) was a composite of true *hoplogaster* and a northern form from which *hoplogaster* was probably derived — for they are separable only on subcaudal counts and relative tail lengths. *C. neglectus* of Boulenger (1894a) was likewise a composite of the same two reptiles, for Boulenger separated his "*neglectus,*" whose ventrals were more or less distinctly keeled, from his "*hoplogaster,*" in which there were no trace of keels. Actually every gradation in this character is to be found throughout the range of both snakes. In recent times Bogert (1940) was the first to point out that *neglectus* Peters is indistinguishable from *hoplogaster* Günther.

The type of *oldhami*, whose ventral and subcaudal counts are unknown, is no longer in the collection of the Indian Museum as I am informed by its Director; neither can it be found in the British Museum, says Mr. J. C. Battersby. Dr. V. FitzSimons concurs (letter of 4.xii.50) in the assignment of his (1948a) "*natalensis*" from the Drakensberg, to *hoplogaster*.

[72] Not 228 by my measuring (A.L.).

*Dentition.* Maxillary teeth numbered 27 in two Rungwe snakes examined by Bogert (1940); apparently 25 and 26 respectively in skulls from Lake Rutamba and Ujiji studied by me, the last few teeth being enlarged.

*Hemipenis.* Not bifurcate; sulcus spermaticus undivided; basal spines large, merging on the middle third into reticulate calyces which grade into papillae towards the tip, which extends to the eighth caudal (Bogert).

*Sexual dimorphism.* Negligible, owing to the considerable overlap in the number of subcaudals, though there is undoubtedly an average difference.

*Breeding.* On March 3, at Mwaya, a ♀ held 5 eggs about 28 x 8 mm.

On October 1, at Nyange, a ♀ held 6 eggs about 20 x 7 mm.

Between October 9-29, at Vituri, a ♀ held 3 eggs about 34 x 10 mm.

On December 18, at Chitala, a ♀ held 6 eggs about 20 x 28 mm.

On February 12, at Chowe, a hatchling measured over 193 (140 + 53) mm. It is possible that the Vituri snake had already laid some of her clutch. Günther (1894a), without giving a date, mentions 5 eggs as ready for extrusion by a Shire Highlands snake.

*Diet.* Lizards and frogs. More specifically, a gecko (*Hemidactylus persimilis*) in the stomach of a Bagamoyo specimen; at Dar es Salaam I watched a captive snake take a gecko (*Lygodactylus p. picturatus*); FitzSimons (1939b) notes a Chirinda Forest reptile had eaten a gecko (*L. capensis*) and frog (*Arthroleptis s. stenodactylus*); several frogs of this same race were in Kitaya snakes, and I caught a Bagilo snake with an *A. s. whytii* in its mouth, recovered a second *whytii* from a Vituri specimen; and a third *whytii* at Ilolo; *A. reichei* at Kigogo; three out of four captive green snakes died after making heavy meals of *Rana m. mascareniensis.* A Nyange snake held a frog, a buprestid beetle and a grasshopper, with the possibility that digestion might have released the insects from the frog's stomach.

*Parasites.* Immature encysted worms (*Acanthocephala* sp.) were present on the outer wall of the intestinal tract of a Bagilo snake which held an adult ♀ ; several Nyange snakes, infested with subdermal cysts, died a few days after being brought in by natives; Vituri specimens were also parasitized.

*Enemies.* One, at least, was eaten by a *Thelotornis k. kirtlandii* that at first shared the vivarium with some green snakes.

*Aestivation.* At the height of the dry season Neave dug one from a termitarium on the bank of the Loangwa River, at which time the ground "was so hard that it could hardly have entered except during the previous rains" (Boulenger, 1907a).

*Habitat.* Southeastern Green-Snakes are very adaptable, being found on the coastal plain, upland savanna, or montane forest, their distribution being governed by conditions sufficiently moist to support the frogs on which they subsist. Consequently they frequent marshes, ponds, and rivers, being as adept at swimming as they are at climbing. F. W. FitzSimons (1912) remarks that when a frog is captured in the water, the snake swims ashore and glides up the bank carrying its prey well off the ground. I (A.L.) found one on the thatch of a watcher's hut in a rice swamp, and many on the fringe of, or in clearings in, rain forest. According to Cott (1935) they abound among the borassus palms near the mouth of the Zambezi.

*Localities.* **Tanganyika Territory:** *Amboni near Tanga; *Bagamoyo; *Dar es Salaam; *Ilolo; Kibongoto (Kibonoto); Kilimanjaro Mtn.; *Kilwa; *Kitaya; Kitopeni; *Lake Rutamba; *Liwale; *Magrotto Mtn.; Marangu; *Mikindani *Morogoro; *Mwaya; *Nchingidi; Rungwe Mtn.; *Ruponda; Tanga; Tukuyu (as Langenburg) *Tunduru; Uhehe; *Ujiji; *Uluguru Mtns.—*Bagilo—*Nyange—*Vituri; Uzungwe Mtns.—*Kigogo; Wanga (as Wange). **Zanzibar:** Mafia Id. only. **Mozambique:** Beira; Boror (as Prazo Boror); Caia; Charre; Fambani; Jeowesa; Lourenco Marques; Mozambique; Quilimane. **Nyasaland:** *Chitala River; *Cholo Mtn.; *Chowe; *Fort Johnston; Karonga; Mandala Hill, Blantyre; *Misuku Mtns.; Mlanje Mtn.—*Ruo River; *Nchenachena; *Nchisi Mtn.; Shire Highlands; *Zomba Mtn. **Belgian Congo**[73]: Bukena; Elizabethville; Ganza; Inkan-

[73] Lukafu being the only Congo locality from which I have seen a specimen, all but 2 of the remaining 42 are based on identifications by de Witte (1953), whose report should be consulted for more precise locality data.

gala; Kabenga; Kabwe; Kakyelo on Luombwa River; Kalule-North River; Kamina; Kande River; Kankala River; Kanonga River; Kanzenze; Kapiri; Kateke River; Katentania; Kaswabilenge; Kilwezi River; Kimiala River; Lofoi; Lubumbashi; *Lukafu; Lukima River; Lukonzolwa; Lukuga-Niemba confluence; Lupiala River; Lusinga; Mabwe, Lake Upemba; Mpala; Munoi; Musosa; Ngayu; Nyonga; Nyunzu; Panda; Sakania; Sandoa; Sanga River; Senze River; Seram Station. **Belgian Ruanda-Urundi:** Mosso Camp, Rutana Territory. **Northern Rhodesia:** Boruma (as Boroma, Zambezi:1898); Broken Hill, Kafue River; Kazungula; Loangwa River; Lungasa; Luapula River; Macubu; Mashie's; Mterize River; Namaliya's; Upper Zambezi River; Victoria Falls; Zambezi Plains. **Southern Rhodesia:** *Chirinda Forest; *Mazoe; *Rietfontein; Salisbury[74]; Vumba Mtn. **Transvaal:** Barberton; Lydenburg; Middleburg; *Pretoria; *Pretoria West. **Natal:** Drakensberg; *Durban; Lower Illovo River; Merebank; Mseleni, Zululand; Port Natal = Durban (type locality); Ubombo; *Umvoti River; Vryheid. **Cape Province:** "Cape Colony"; East London; Knysna; Orange River; Pondoland; Port Elizabeth; Port St. Johns.[75]

*Range.* East Africa south of about 5° S., i.e. south of the Usambara Mountains, Tanganyika Territory, south to Durban, Natal, west to Port Elizabeth, Cape Province, and north through the Rhodesias to the eastern Belgian Congo.

### Philothamnus irregularis battersbyi Loveridge

1878a. *Philothamnus hoplogaster* Peters (not Günther), p. 206.
1892. *Philothamnus neglectus* Matschie (not Peters), p. 110.
1893. Pfeffer (part), p. 84 (omit Quilimane).
1894a. *Chlorophis hoplogaster* Boulenger (part; not Günther), p. 93 (Victoria Nyanza only).
1896. Tornier, p. 69.
1897a. Tornier, p. 69 (reprinted).

[74] Identification checked by Dr. Walter Rose. More recently D. C. Broadley writes me (20.ix.56) that he has collected examples of both *hoplogaster* and *i. irregularis* at Salisbury; both species have also been reported as occurring in Chirinda Forest.

[75] The Wynberg record of Boulenger (1910b) is obviously erroneous, for *hoplogaster* does not occur in western Cape Province. Evidently Boulenger never saw the specimen on which the record was based, for W. Rose informs me (9.xi.56) that it is an example of *Hemirhagerrhis nototaenia.*

1897b. Tornier, p. 65.
1902d. Boulenger, p. 446.
1910b. Boulenger (part), p. 507 (part key & range).
1910a. Sternfeld, p. 18 (Bukoba).
1912. FitzSimons, F. W. (part), pp. 86, 87, 92 (part key & range).
1916a. Loveridge, pp. 78, 84.
1918a. Loveridge, pp. 333.
1924b. Loveridge, p. 5.
1929. Hecht (part), p. 332 (part key & range).
1929b. Loveridge, p. 22.
1929a. Werner (part), p. 100 (part key & range).
1933b. Loveridge (part), p. 236 (omit Tanganyika localities).
1936j. Loveridge, p. 245.
1936. Pitman, p. 275.
1938a. Pitman, p. 305.
1939a. Scortecci, p. 274.
1942b. Bogert, p. 2.
1942e. Loveridge, p. 271.
1894a. *Chlorophis neglectus* Boulenger (part; not Peters), p. 94 (Lamu; Mkonumbi; and Teita in Kenya; Zanzibar Coast).
1894c. Günther, p. 88.
1895. Günther, p. 527.
1896a. Boulenger, p. 553.
1896d. Boulenger (part), p. 631 (omit Nyasaland localities).
1896. Tornier, p. 69.
1897a. Tornier, p. 69 (reprinted).
1908c. Sternfeld, p. 240.
1908e. Sternfeld, p. 243.
1909a. Boulenger, p. 193.
1910b. Boulenger (part), p. 507 (part key & range).
1910a. Sternfeld (part), p. 18 (Kagera).
1910. Meek, p. 406.
1911. Lampe, p. 193.
1911. Lönnberg, p. 23.
1911b. Nieden, p. 442.
1912. FitzSimons, F. W. (part), p. 86 (part key & range).
1912. Hobley, p. 48.
1913. Lönnberg & Anderson, p. 4.
1916a. Loveridge, pp. 79, 84.
1916b. Loveridge, p. 118.
1917b. Loveridge, p. 180.
1918a. Loveridge, p. 332.
1923a. Loveridge, p. 26.

1923e. Loveridge, p. 878.
1924b. Loveridge, p. 5.
1925a. Calabresi, p. 106 (as *Clorophis*).
1925a. Angel, p. 32.
1927. Calabresi, p. 53 (as *Clorophis*).
1928c. Barbour & Loveridge (part), p. 115 (Usambara locs. & data).
1929. Hecht (part), pp. 332, 333 (part key & range).
1929h. Loveridge, p. 22.
1929a. Werner (part), p. 100 (part key & range).
1934c. Mertens, p. 169.
1936h. Loveridge, p. 30.
1936j. Loveridge, p. 246.
1936. Pitman, p. 276, pl. v, fig. 3; pl. E., fig. 5.
1937f. Loveridge, pp. 489, 493, 496, 503.
1937. Uthmöller, p. 108 (omit range).
1938a. Pitman, p. 305.
1938b. Pitman, pp. 89, 90, 305 (reprinted, pls. as in 1936).
1938. Uthmöller, p. 43.
1941a. Uthmöller, p. 26.
1941b. Uthmöller, p. 233.
1946a. Loveridge, pp. 97, 108.
1918. *Philothamnus semivariegatus* Calabresi (not Smith), p. 124.
1929h. *Chlorophis* sp. Loveridge, p. 23.
1946. Blom-Bjorner, 1945, p. 159.
1948. "Green Grass Snake" Kingdon, p. 10.
1949a. *Chlorophis irregularis hoplogaster* Parker (not Günther), p. 61.
1951a. *Chlorophis irregularis battersbyi* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 190: Sipi Forest at 6,000 feet, Mount Elgon, eastern Uganda
1951c. Loveridge, pp. 4, 7.

*Common Names.* Northeastern Green-Snake (English); *emun* (Karamojong); *homboka* (Pokomo); *naranyase* (Gishu); *newandegala* (Ganda).

*Description.* Preoculars 1, rarely 2[76]; postoculars 2, rarely 3[77]; temporals 1 + 1 or 1 + 2, rarely 1 + 3[78] or 2 + 2[79]; upper

[76] Two in two Kaimosi snakes (M.C.Z. 40501; 40504).

[77] Three in a Butandiga snake (M.C.Z. 40492), while the lower postocular is fused with the fifth labial on one side of a Naivasha snake (U.S.N.M. 41701).

[78] On one side of a Sanya snake (*fide* Uthmöller:1938).

[79] On one side of a Butandiga snake (M.C.Z. 40489).

labials 7-9,[80] rarely the third and fourth, usually the fourth and fifth, occasionally the fifth and sixth, entering the orbit; lower labials 8-11, the first four, five or six in contact with the anterior sublinguals; midbody scale rows 15; ventrals 147-177 (♂♂ 147-169; ♀♀ 153-177); anal divided, rarely entire[81]; subcaudals 90-120 (♀♀ 90-111; ♂♂ 100-120).

For characters common to all species, and synopsis of scale counts, see pp. 49-52, 55.

*Color.* Above, pale or dark green, the interstitial skin black; some scales with a white basal spot, others with or without black edging. Below, chin and throat white; remainder white, yellowish, or pale green.

*Size.* Length of ♂ (M.C.Z. 40172) 841 (588 + 253) mm., and ♀ (M.C.Z. 40155) 1045 (762 + 283) mm., both from Sipi, Mt. Elgon.

*Remarks.* It will be noted that this northeastern race of *irregularis* usually attains to a greater length than does the southern *hoplogaster*, with which it has long been confounded. Thus for a *hoplogaster* ♂ the maximum is 720 mm., for a ♀ 945 mm., while for an *irregularis battersbyi* ♂ the maximum is 841 mm., for a ♀ 1045 mm.

Though the northeastern *battersbyi* has so long been confused with *hoplogaster* (Günther) or its synonym *neglectus* (Peters), with which it agrees in the number of labials entering the orbit, and to which it presumably gave rise, when sexed it may be distinguished as follows:

Subcaudals in ♀♀ 73-98, in ♂♂ 87-106; range: Eastern Congo and East Africa from the Usambara Mountains, south through the Rhodesias and Mozambique to Natal ..... *hoplogaster*

Subcaudals in ♀♀ 90-111, in ♂♂ 100-120; range: East Africa from the Usambara Mountains north through Kenya to Ethiopia, west to the Nile and Uganda where it merges with typical *irregularis* ..... *i. battersbyi*

[80] 7 Labials, 3 & 4 entering on both sides (Nairobi: U.S.N.M. 49007). 7 labials, 4 & 5, entering on 1 side (Nairobi: U.S.N.M. 40985). 8 labials, 4 & 5 entering on 205 sides. 8 labials, 5 & 6 entering on 1 side (Nairobi: U.S.N.M. 40985). 9 labials, 5 & 6 entering on 29 sides.

[81] Entire in a Naivasha snake (U.S.N.M. 41701).

From typical *irregularis* it is separable only on the upper labials as follows:

Two labials (rarely the 3rd and 4th, normally the 4th and 5th, occasionally the 5th and 6th) enter the orbit in all northeastern material ..... *i. battersbyi*

Usually 3 labials (rarely 3rd, 4th and 5th, normally 4th, 5th and 6th, rarely the 5th, 6th and 7th) but occasionally (chiefly among Angolan snakes and not more than 5% of the West African population) only 2 labials (the 4th and 5th, or 5th and 6th) enter the orbit ..... *i. irregularis*

The snake from Gelib and Margherita referred to by Calabresi (1918) as a ♂ *"semivariegatus"* cannot be that species if the low ventral count is correct. It does agree in both ventrals (155) and subcaudals (90) with ♀ *i. battersbyi*, but if a ♂ the tail must be truncated.

Notes on labial variation, based on other material, will be found in Loveridge (1936j, p. 245).

*Sexual dimorphism.* Reference to the description (*vide supra*) reveals only a slight average difference in the number of subcaudals as between the sexes.

*Breeding.* More than a dozen detailed records will be found under *"hoplogaster"* and *"neglectus"* in Loveridge (1936j, pp. 246-247). These, together with earlier records, would seem to indicate that in Uganda and western Kenya, from 4 to 8 eggs are laid towards the end of the lesser (November-December) or greater (February-March) rains, but that in the coastal belt of Kenya eggs are ready for laying about June. The single record of July 16 from Ukerewe Island, Lake Victoria, where only 2 eggs (measuring 29 x 8 mm.) were in the oviducts of a large female, suggests that other eggs of the series had been deposited already.

*Diet.* At various tims I have recorded stomach contents comprising the following lizards: *Cnemaspis a. elgonensis; Chamaeleo b. hochnelii; Mabuya s. striata; Ablepharus wahlbergii* and *Lacerta jacksoni*, and frogs: *Rana a. edulis, R. o. gribinguiensis* and *Hyperolius rossii*, sometimes several examples in one snake, at other times several snakes having swallowed the same species.

An interesting account of a struggle between a "vivid green grass snake" and a five-or-six-inch catfish (*Amphilius*) has been

furnished by Major J. Kingdon (1948). He was near Thego Ford, Nyeri Station, when his attention was attracted by a violent commotion in a shallow water furrow above whose surface waved the coils of a snake. As Kingdon approached the spot, the reptile pulled the fish from the runnel and started with it across the river. On reaching deeper water, however, the fish took control and the combatants were carried down stream to shallower water where the snake regained the advantage and, by entwining among the rocks, succeeded, though only with a great effort, in dragging the *Amphilius* along. Both appeared exhausted by the struggle, especially the snake, which was periodically submerged by the weight of its prey. Eventually the fish, by diving among sunken twigs, achieved its freedom and swam off down the runnel.

*Parasites.* An immature ascarid in a Nairobi snake (Loveridge:1923e), others encysted in the stomach wall of a Kaimosi reptile (1936j).

*Enemies.* I recovered one of these green-snakes from the stomach of a harrier-eagle (*Circactus g. gallicus*) shot at the foot of Mt. Debasien, while two others were taken from the crop of a *C. cinerascens* by Blom-Bjorner (1946).

*Temperament.* One of a pair of green snakes that I caught bit sufficiently hard to draw blood (1917b).

*Habits.* Two, basking on bushes overhanging Nairobi River, escaped by dropping off into the water (1916b).

*Habitat.* One was resting on a lily pad far out in a swamp where it was probably hunting frogs; in this same flooded area another was associated with two Variegated Bush-Snakes (*Philothamnus s. semivariegatus*) in a small doom palm. While this was on the coastal plain, *battersbyi* is as much at home on upland savanna or montane forest-edge. As a variation of its usual habitat, one put its head out of a leather hairbrush-case on a Nairobi dressing table that it had reached through an open casement.

Uthmöller (1941b) believed that this and certain other snakes actually thrive and multiply when land is cleared for the cultivation of bananas, coffee or maize, and disappear when the plantations revert to bush. I would suggest that their apparent prev-

alence in cultivated areas is due to the reptiles being more readily seen and killed by the numerous Africans employed about a plantation.

*Localities.* **Sudan:** *Torit. **Ethiopia:** Abbai (? Lake Abaya, Tancredi Expedition to Lake Tana); Addis Ababa; Gadat, Gofa; Gondar; Guder; Let Marefia, Shoa. **Somalia:** Belet Amin; possibly Gelib and Margherita, west of Juba River (if the *"semivariegatus"* of Calabresi is *battersbyi*); Kismayu. **Uganda:** Kagera; Mabira Forest—*Mubango; *Mt. Debasien; *Mt. Elgon—*Butandiga, *Sipi; *Ntenjeru near Sesibwa River. **Kenya Colony:** *Athi River; *Fort Hall; *Juja; Kabete; *Kaimosi, Kakamega (Kakumega); *Kau; Kavirondo; Kenya Mtn.; *Kenya Province; Kibwezi; *Kijabe; *Kirui's Village; Kitui; *Lake Elmenteita; Lake Naivasha; *Lake Peccatoni; Lamu; Masai Reserve; Meru Boma; *Mkonumbi; Mtito Andei; *Nairobi; Nakuru; *Ngatana; Nyeri Station; Teita; Thika; Tumutumu; *Voi; Wambugu; *Witu; Yala River **Tanganyika Territory:** Bukoba; Gomberi; *Ikizu; *Korogwe; Lake Victoria; Marangu; *Matembo; Sanya; *Ukerewe Id.; Usambara Mtns.—*Amani, Bulwa, *Bumbuli, Derema, Lewa, *Mlalo near Höhenfriedeberg, Nguelo; "Zanzibar Coast" (Boulenger 1894a: probably Usambara).

*Range.* East Africa (east of 33° E., south of 15° N., and north of 5° S.). More specifically, the Sudan (east of the Nile), east through Ethiopia to Somalia, south through Uganda and Kenya Colony to (and including) the Usambara Mountains of northeastern Tanganyika Territory, west to Lake Victoria.

### Philothamnus irregularis ornatus Bocage

1872. *Philothamnus ornatus* Bocage, Jorn. Sci. Lisboa, **4**, p. 80: Huilla, Angola (restricted by Bogert:1940).
1882c. Bocage, p. 15, fig. 6.
1884b. Sauvage, p. 201 (as *Philothalmus* in French Congo list).
1895a. Bocage, p. 93, pl. xii, figs. 1a-c.
1896a. Bocage, p. 78.
1897a. Bocage, p. 200.
1894a. *Chlorophis ornatus* Boulenger, p. 93.
1896d. Boulenger, p. 631.
1905c. Boulenger, p. 112.

1915a. Boulenger, p. 205.
1919a. Boulenger, p. 281.
1921a. Angel, p. 42.
1929. Hecht, p. 332.
1929a. Werner, p. 100.
1931. Monard, p. 103.
1933f. Angel, p. 109.
1937b. Monard, pp. 113, 119.
1940. Bogert, p. 51.
1940b. Monard, p. 148.
1950b. Villiers, p. 80.
1937b. *Chlorophis hoplogaster* Monard (not Günther), pp. 114, 120.
1951c. *Philothamnus irregularis ornatus* Loveridge, pp. 4, 8.

A further citation of "*ornatus*" will be found under *heterolepidotus*.

*Common Name.* Ornate Green-Snake (Loveridge).

*Description.* Preocular 1; postoculars 2; temporals 1 + 1, rarely 1 + 2[82]; upper labials 8-10, the third and fourth, normally the third, fourth and fifth, rarely fourth and fifth, or fourth, fifth and sixth, entering the orbit; lower labials 10, the first 5 or 6 in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 150-166 (♂ 150; ♀♀ 160-161); anal divided; subcaudals 85-106 (♀♀ 99; ♂ 106).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above, iridescent green or bronze green, the interstitial skin black, a few scattered black spots on the nape and a broad, usually yellow-edged, chocolate-brown, vertebral band extending from head to end of tail; this band occupies the median series of dorsal scales and encroaches on those on either side; a few scales may be flecked with white. Below, yellowish cream, uniform, or the posterior margins of some ventrals brownish; tail greenish.

*Size.* Length of ♂ (A.M.N.H. 51772) 610 (405 + 205) mm.; larger ♀ (P.M. 20-100) 693 (480 + 213) mm., both surpassed by an unsexed cotype (Bocage) of 710 (510 + 200) mm.

*Remarks. P. i. ornatus* is apparently separable from typical *irregularis* only by its striking coloration, which resembles that

[82] Only in the Bimbi snake referred to "*hoplogaster*" by Monard (1937b).

of the perfectly distinct *Philothamnus s. dorsalis* Bocage of the same general region. *P. i. ornatus* occupies a fairly well-defined area in southwestern Angola where it is partly surrounded by typical *irregularis* as it approaches the limits of its range in the southwest.

Possibly undue emphasis has been laid on the striking coloration of *ornatus* and a more representative southwestern race of *irregularis* would embrace all Angolan material possessing a low number of ventrals and subcaudals. This point could be settled by someone assembling all available Angolan material of the genus.

I have seen the specimen of *ornatus* recorded from neighboring Northern Rhodesia by Angel, but the alleged "*ornatus*" from the Congo proved on examination to be a misidentified *heterolepidotus*. I also would question Sauvage's listing of it from the French Congo, though it may indicate the recrudescence of a recessive pigmentation.

Bocage himself (1872) listed one of his three cotypes as coming from Cacheu (Cachéo), a river and bay in northern Portuguese Guinea. Later (1896a) he gives Bissau as the type locality in his list of types from Portuguese Guinea in the Lisbon Museum. I am inclined to suspect an error in labeling, for in a later list Bocage returns to Cacheu. Probably the specimen originally came from Angola, from which country 10 specimens are now known, justifying Bogert's (1940) action in restricting the type locality to Huilla, from whence we have a cotype. There is but a single example of *ornatus* in the British Museum.

*Dentition.* Maxillary teeth 26, slightly increasing in size posteriorly (Bogert).

*Hemipenis.* Not bifurcate; sulcus spermaticus undivided; basal spines large, blunt, merging into 6 flounces which occupy the middle third; passing on the terminal third into reticulate calyces which grade into papillae towards the tip, which extends to the eighth caudal (Bogert).

*Localities.* **Angola:** Benguela to Bihe; Bimbi; Caconda; Caluquembe (Kalukembe); Chimporo; Cunene; Cutato (Kutatu); Huambo; *Huilla. **Northern Rhodesia:** *Lealui (Lialui).[83]

*Range.* Southwestern Northern Rhodesia west to southwestern Angola.[83]

[83] See Remarks regarding its listing from **French Congo** by Sauvage (1884) and **Portuguese Guinea:** Cacheu (Bocage:1872).

### Philothamnus irregularis irregularis (Leach)

*Series I. Mostly typical, having 3 labials entering the orbit.*

1789. *C(oluber) Caeruleus* Lacépède (not Linnaeus, 1758, p. 218, No. 189), Hist. nat. Serpens, **2**, pp. 100, 276: Cap Vert.
1803c. *Coluber caeruleseens* Daudin (not Linnaeus, 1758, p. 227, No. 385), Hist. nat. Rept., **7**, p. 54: new name for *caeruleus* Lacépède from "Cap Verd."
1818. *Coluber caesius* Cloquet, Dict. Sci. nat. (Paris), **11**, p. 201: new name for *caeruleus* Lacépède (Suppressed: cf. *Remarks*).
1819. *Coluber irregularis* Leach, in Bowdich, Miss. Ashantee, p. 494: Fantee, Gold Coast.
1840. *Dendrophis* (*Philothamnus*) *albo-variata* A. Smith, Ill. Zool. S. Africa, Rept., pl. lxiv, figs. 3-3b; pl. lxv: South Africa towards Tropic of Capricorn (also Ghana; Sierra Leone; Gambia).
1843. *Dendrophis Chenonii* Reinhardt, Dansk. Vidensk. Selsk. Skrift., **10**, p. 246, pl. i, figs. 13-14: Guinea.
1854a. *Leptophis Chenonii* Duméril & Bibron, **7**, p. 545.
1860. Duméril, A., p. 199.
1866a. Bocage, p. 48.
1881. Jan, pl. i, fig. 2.
1858. *Ahaetulla irregularis* Günther (part), p. 152.
1863c. Günther, p. 285.
1874. Reichenow, p. 292.
1882b. Müller, p. 169.
1885. Müller, p. 683.
1893. Günther, p. 555.
1898. Johnston, p. 361a.
1867b. *Philothamnus albovariatus* Peters, p. 236.
1882c. Bocage, p. 19.
1875a. *Philothamnus irregularis* var. *longifrenatus* Buchholz & Peters, Monatsb. Akad. Wiss. Berlin, p. 199: Cameroon.
1877c. *Philothamnus irregularis* Peters, pp. 615, 620.
1881b. Boettger, p. 396.
1881d. Peters, p. 149.
1882c. Bocage, pp. 3-4, fig. 1.
1884a. Rochebrune, p. 172 (ignored).
1887a. Bocage, p. 205.
1888a. Boettger, p. 61.
1890. Büttikofer, p. 446.
1895a. Bocage (? part), p. 85, pl. xii, figs. 2a-2c (? *angolensis*).
1896a. Bocage, pp. 78, 92.

1896b. Bocage, p. 112.
1896c. Bocage, p. 176.
1905. Ferreira, p. 167.
1952b. Villiers, p. 888.
1954d. Laurent, p. 305.
1885. *Ahaetulla* (*Leptophis*) *fraenata* Müller, p. 684 (? lapsus: not *A. frenatus* Günther which = *Uromacer frenatus* of Haiti).
1888a. *Ahaetulla emini* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 51: "Monbuttu," = Mangbetu Belgian Congo.
1888b. Günther, p. 325.
1888b. *Ahaetulla shirana* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 326: Blantyre Mission, Shire River, Nyasaland.
?1893. *Philothamnus Güntheri* Pfeffer, Jahrb. Hamburg. Wiss. Anst., **10**, p. 85, pl. i, figs. 3-5: Quilimane, Mozambique.
1905. Ferreira, p. 168 (Angola).
1895. *Chlorophis Güntheri* Günther, p. 528 (key).
1895. *Chlorophis shirana* Günther, p. 528 (key).
1891a. *Chlorophis irregularis* Boulenger, p. 306.
1894a. Boulenger (part), p. 96 (omit locality Ugogo).
1895. Günther, p. 528.
1896d. Boulenger, p. 631.
1896b. Mocquard, p. 45.
1896c. Mocquard, p. 59.
1896. Peracca, p. 2.
1896. Tornier, p. 70, fig. D.
1897b. Boulenger, p. 278.
1897c. Boulenger, p. 801.
1897. Sjostedt, p. 35.
1897. Tornier, p. 65.
1897b. Werner, p. 398.
1898. Boettger, p. 58.
1898. Johnston, p. 361a.
1898. Sclater, p. 99.
1898a. Werner, p. 209.
1899a. Werner, pp. 147, 149.
1900b. Boulenger, p. 452.
1902d. Boulenger, p. 446
1902a. Werner, pp. 334, 344.
1903a. Ferreira, p. 10.
1905c. Boulenger, p. 112.
1906i. Boulenger, p. 213.
1908a. Sternfeld (part), p. 425 (omit Bipindi).
1908b. Sternfeld, pp. 214, 230.

1909a. Chubb, p. 595.
1909b. Chubb, p. 35.
1909. Gendre, p. cvi.
1909. Peracca, p. 172.
1909a. Sternfeld, p. 14.
1909b. Sternfeld, p. 15.
1910b. Boulenger, p. 508.
1910a. Sternfeld (part), p. 19 (omit Ugogo).
1910d. Sternfeld, p. 64.
1911c. Boulenger, p. 165.
1911. Lepri, p. 324.
1912. FitzSimons, F. W., p. 87.
1912b. Sternfeld, p. 384.
1912c. Sternfeld, p. 270.
1915a. Boulenger, p. 205.
1915c. Boulenger, p. 623.
1916f. Chabanaud, p. 371.
1917b. Chabanaud, p. 11.
1917. Sternfeld, p. 468.
1919a. Boulenger, p. 282.
1921a. Angel, p. 42.
1921a. Chabanaud, p. 468.
1921b. Chabanaud, p. 524.
1922. Aylmer, p. 15.
1923c. Loveridge, p. 878.
1923. Schmidt, p. 76.
1927. Calabresi, p. 53.
1927d. Witte, p. 323.
1928. Cott, p. 953.
1929. Flower, p. 203.
1929. Hecht, pp. 331, 334.
1929a. Werner, p. 101.
1930a. Barbour & Loveridge, p. 772.
1931. Monard, p. 104.
1932a. Parker, p. 219.
1933f. Angel, p. 108.
1933. Flower, p. 806.
1933. Schouteden, p. 236.
1933m. Witte, p. 89.
1934c. Mertens, p. 169.
1934. Pitman, p. 294.
1934a. Schwetz, pp. 380, 383.
1934b. Schwetz, supp. p. (24).

1935a. Corkill (part), p. 17 (part *heterolepidotus*).
1935. Cott, p. 966.
1936h. Loveridge, p. 30 (part *heterolepidotus*).
1936j. Loveridge (part), p. 247 (omit Kaimosi specimens).
1936c. Parker, p. 125.
1936. Pitman, p. 278, pl. v, fig. 5, pl. E, fig. 3.
1937a. FitzSimons, V. F., p. 273.
1937e. Loveridge (part), p. 273.
1937f. Loveridge, pp. 489, 496, 503.
1937b. Monard (part), pp. 114, 121 (tentatively omitting *angolensis*).
1938c. Mertens, p. 439.
1938a. Pitman, pp. 306, 328.
1938b. Pitman, pp. 23, 39, 87, 91-93, 98, 294, 306, 328 (reprinted).
1939b. FitzSimons, V. F., p. 22.
1940. Bogert (? part), p. 53 (? omit one of Capelongo series).
1940b. Monard, p. 175.
1941. Themido, pp. 4, 10.
1941. Witte (part), pp. 184-198 (part *heterolepidotus*).
1942e. Loveridge, p. 272.
1945. Leeson, p. 1 (key).
1950f. Laurent, p. 128.
1950. Leeson, pp. ix, 39, 40, 66, 133, fig. 17.
1950. Rose, p. 272.
1950b. Villiers, p. 81, figs. 96-97.
1951. Monard, p. 149.
1955. Rose, pp. 93, 97 (faulty key).
1894a. *Chlorophis emini* Boulenger (part), p. 92, pl. v, fig. 1 (omit Sudan specimens which are *heterolepidotus*).
1895. Günther, p. 528 (key only).
1900. Flower, p. 968.
1902d. Boulenger, p. 446.
1908c. Boulenger, p. 5.
1908a. Sternfeld, pp. 407, 424.
1908. Werner (1907), p. 1871.
1909b. Boulenger, p. 303.
1909g. Boulenger, p. 246.
1909b. Sternfeld, p. 15.
1910. Peracca, p. 4.
1910. Roux, p. 99.
1910a. Sternfeld, p. 18, fig. 17.
1911c. Boulenger, p. 165.
1912c. Sternfeld, p. 268.
1915a. Boulenger, p. 204.

1915c. Boulenger, p. 622.
1915d. Boulenger, p. 648.
1916f. Chabanaud, p. 371.
1917b. Chabanaud, p. 11.
1917a. Phisalix, p. 334.
1922a. Angel, p. 39.
1929. Heeht, pp. 332, 333.
1929. Pitman, p. 145.
1929a. Werner, p. 100.
1933h. Loveridge, p. 236.
1933. Schouteden, p. 236.
1933j. Witte, p. 123.
1933m. Witte (part), p. 88 (omit Elisabethville and Kanzenze).
1934c. Mertens, p. 155.
1935a. Corkill (part), p. 16.
1939. Brien, p. 130.
1892a. *Philothamnus irregularis* var. *lagoensis* Bocage (not Günther), p. 183.
1896a. *Philothamnus irregularis* var. *Güntherii* Bocage, p. 92 (Boror).
1902a. *Chlorophis heterolepidotus* Werner (part), p. 344.
1933m. Witte (part), p. 89 (Faradje and Mahagi).
1940b. Monard, p. 175 (Portuguese Guinea).
1913. *Chlorophis hoplogaster* Hewitt & Power (not Günther), p. 162.
1941. Witte, p. 184.
1923. *Chlorophis bequaerti* Schmidt (part), p. 75 (paratype ♀).
1932. *Chlorophis vernayi* FitzSimons, V. F., Ann. Transvaal Mus., **15**, p. 38: Maun, Thamalkane River, British Bechuanaland.
1935b. FitzSimons, V. F., p. 132, fig. 1.
1933m. *Chlorophis heterodermus* Witte (part: not Hallowell), p. 89 (Albertville).
1941. Witte (part), p. 198 (Burunga).
1938d. *Philothamnus nitidus* Loveridge (not Günther), p. 57.
1948a. Villiers, p. 202.
1950a. Villiers, p. 62.
1950b. Villiers (part), p. 82, figs. 98-99.
1951a. Villiers, p. 822.
1954b. Villiers, p. 1240.
1946. *Philothamnus semivariegatus nitidus* Orton & Morrison (not Günther), p. 16.
1951c. *Philothamnus irregularis irregularis* Loveridge, pp. 4, 8.
1951d. Loveridge, p. 88.
1953c. Loveridge, p. 261.
1953. Witte, p. 189, fig. 55, pl. xvii, fig. 1.

1954. Angel, Guibé, Lamotte & Roy, p. 392.
1954b. Laurent, p. 47.
1954d. Laurent, p. 296.
1954b. Villiers, p. 1239.
1955. Witte, p. 216.
1956. Laurent, p. 160, fig. 26, pl. xviii, fig. 1.
1953. *Philothamnus hoplogaster* Witte (not Günther), fig. 52 only.
1955a. *Chlorophis irregularis irregularis* Mertens, p. 91.

Further citations of "*irregularis*," "*emini*," and "*bequaerti*" will be found under *natalensis, heterolepidotus, s. thomensis* and *s. semivariegatus.*

*Series II. Aberrant individuals with 2 labials entering orbit.*

1881. *Leptophis Chenonii* var. *albovariata* Jan (not A. Smith), No. 50, pl. i, fig. 1: (no locality mentioned).
1881. *Leptophis Chenonii* Jan (not Duméril & Bibron), No. 50, pl. 1, figs. 3-4: (no locality mentioned).
1882c. *Philothamnus angolensis* Bocage, Jorn. Sci. Lisboa, **9**, p. 7: Capangombe, Angola.
1897a. Bocage, p. 200.
1884b. *Philothamnus hoplogaster* Sauvage (not Günther), p. 201 (French Congo).
1887a. Bocage (not Günther), p. 186 (San Salvador).
1887h. Boulenger (part), p. 176 (Damaraland only).
1887h. *Philothamnus natalensis* Boulenger (not A. Smith), p. 176 (Damaraland only).
1894a. Boulenger (part), p. 95.
1910b. Sternfeld (part), p. 19.
1894a. *Chlorophis angolensis* Boulenger, p. 95 (no material).
1915a. Boulenger, p. 205.
1929. Hecht, p. 333.
1929a. Werner, p. 100.
1937b. Monard, p. 114.
1894a. *Chlorophis hoplogaster* Boulenger (part), p. 93 (Damaraland).
1896b. Mocquard (as *noplogaster*, not Günther), p. 45 (Abiras).
1910b. Sternfeld, p. 19 (Damaraland).
1925b. Calabresi, p. 125 (Upper Uele River).
1933m. Witte, p. 88 (Belgian Congo localities).
1937b. Monard, p. 120 (Bimbi).
1941. Witte, p. 184 (Belgian Congo & Ruanda localities).
1951. Monard, pp. 150, 159.

1900. *Philothamnus irregularis* var. *angolensis* Ferreira, p. 51 (Cazengo).
1904. Ferreira, p. 115 (Chingo).
1908a. *Chlorophis neglectus* Sternfeld (not Peters), p. 407 (Yaunde).
1909b. Sternfeld, p. 15 (Yaunde).
1923d. Angel, p. 165 (nr. Loeti River, Angola).
1933m. Witte, p. 88 (6 Belgian Congo localities).
1937b. Monard, p. 114 (repeats Angel's record).
1940a. Mertens, p. 241 (Kaka region, Cameroons).
1951. Monard, p. 150.
1908a. *Chlorophis irregularis* Sternfeld (part), p. 407 (Bipindi).
1908. Werner (1907), p. 1871 (Hellet Nuer).
1917. Sternfeld (? part), p. 468.
1940. Bogert (part), p. 53 (mentions one of 4 Capelongo snakes as aberrant, correctly referring all to typical *irregularis*).

A further reference to "*angolensis*" will be found under *natalensis*.

*Common Names.* Irregular Green-Snake (Corkill) appears to be the most definitive of the seven names proposed by A. B. Cozens, F. W. FitzSimons, Flower and Pitman. *Bourakende* (French Guinea :Mocquard) ; *chilembe* (Caconda :Bocage) ; *emun* (Karamojong :Loveridge) ; *imbindipindi* (Nyakusa :Loveridge) ; *kalembwe-lembwe* (at Dundo :Laurent) ; *kiango* (Casengo :Bocage) ; *mukangalleni* (Bakiga :Pitman) ; *mussola* (Ndallo-Tando : Ferreira) ; *nalwinduwindu* (Misuku :Loveridge) ; *namasamba* (Manganja ; Nyanja ; Yao :Loveridge) ; *nombo* (at Benguela & Quindumbo) ; *nuwandagerra* (Ganda :Pitman) ; *rungu* (Moro Nubas :Corkill) ; *semsari* (Baggara Arabs :Corkill) ; *uango* (Quissange :Anchieta).

*Description.* Preoculars 1, rarely 2[84] ; postoculars 2, rarely 1, 3 or 4[85] ; temporals rarely 1 + 0,[86] usually 1 + 1, frequently 1 + 2, rarely 1 + 3, 2 + 1, 2 + 2[87] or 3 + 2[88] ; upper labials

[84] In a Mt. Debasien (M.C.Z. 40525) and a Bonthe (B.M. 50.i.1.13) snake. The head from "Mtungun, East Africa," figured by Tornier (1896 :70, fig. D) with 2 pre-, 3 post-, and 2 suboculars, if not a *Thrasops j. jacksonii*, is certainly an extraordinarily aberrant individual.

[85] In a Mt. Debasien snake (M.C.Z. 40524), and on one side of a Bel Air snake (C.G. 44-1-9).

[86] On one side of a Misuku Mountains snake (M.C.Z. 51111).

[87] On one side of a Cholo Mountain snake (M.C.Z. 51123) ; also three Sierra Leone specimens (Brit. Mus.), a Camberene, Dakar reptile (*fide* Villiers) and a Chingo snake (*fide* Ferreira).

[88] On both side of an Achimota ♀ (C.N.H.M.).

8-10,[89] the third, fourth and fifth, or fourth and fifth, usually fourth, fifth and sixth, rarely fifth and sixth, or fifth, sixth and seventh, entering the orbit; lower labials 8-11, the first 4, 5, or 6 in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 150-183[90] (♂♂ 150-179; ♀♀ 153-183); anal divided, rarely entire[91]; subcaudals occasionally faintly keeled and notched[92] 87-127 (♀♀ 87-119; ♂♂ 103-127).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above green or olive, the interstitial skin black; on nape and anterior part of back occasionally a longitudinal series of paired black spots which may coalesce to form crossbars; some scales with a white basal spot with, or without, black edging. Below, greenish yellow or very pale green.

*Size.* Length of ♂ (B.M. 84.11.24.5) 1070 (720 + 350) mm., from Sierra Leone; of ♀ (M.C.Z. 51120) 1080+ (785 + 295+) mm, from Cholo Mountain; while the amended measurement of another ♀ (T.M. 18560) 1030 (710 + 320) mm., from as far south as Silinda Mountain, is recorded by FitzSimons (1939b: 22).

*Remarks.* Both *Coluber caeruleus* Lacépède and Daudin's substitute name of *caerulescens* are preoccupied by Linnaean names for very different reptiles from the Cape Verde snake with 170 ventrals. The latter certainly appears to be an *irregularis* with truncated tail (its subcaudals allegedly numbering only 64). Consequently the name *irregularis* Leach, 1819 — which has been

[89] 8 labials, the 3, 4, 5 entering on 9 sides (3 snakes have it on both). 8 labials, the 4, 5 entering on 1 side (L. Mutanda: M.C.Z. 48288). 8 labials, the 4, 5, 6 entering on 1 side (Bundibugyo: M.C.Z. 48279). 9 labials, the 4, 5, 6 entering on 199 sides (94 snakes have it on both). 9 labials, the 5, 6 entering on 4 sides (Mlanje Mtn.: A.M.N.H. 67766 has it on both but too many subcaudals for *hoplogaster*). 9 labials, the 5, 6, 7 entering on 1 side. 10 labials, the 5, 6, 7 entering on 2 sides (Rhino Camp: U.S.N.M. 42479; Chiradzulu: M.C.Z. 51176; on one side of each snake).

[90] 183 recorded by Villiers (1952b) and double-checked by me.

[91] Entire in a snake from the Misuku Mountains (M.C.Z. 51110), another from Mayumbe (M.C.Z. 42912), and a third from Sierra Leone (B.M. 68.5.27.10), etc.

[92] 86 in the type of *vernayi*, but on re-examination FitzSimons finds the tail tip, though terminating in a slender spine, less tapering than in other specimens so possibly lost in early life (26.ii.51); 87 for a Dundo snake (*fide* Laurent) etc., but all those below 90 that I have examined possessed regenerated terminal points.

in general use for almost a century and a half — should yield precedence to *caesius* Cloquet, 1818, which has never been used by any other author. So unfortunate a change was avoided by invoking action by the International Commission on Zoological Nomenclature who ruled that it be suppressed (Opinion 328 of 7.i.1955).

The type *albovariata* A. Smith appears to be lost according to V. F. FitzSimons (1937a).

*C. angolensis* (Bocage; 1882c) cannot be separated from *irregularis* (with which its author later synonymized it) by its loreal being "scarcely longer than deep," for in typical *irregularis* the length of the loreal ranges from 1½ to 2½ times its depth. Bocage based the name on an aberrant *irregularis* in which the third labial was excluded from the orbit. From time to time similar individuals have been recorded as occurring alongside normal *irregularis* throughout much of its range (as here defined) but form less than 5 per cent of the population. They are inseparable from the northeastern population which I have named *irregularis battersbyi*, as *angolensis* cannot be applied to them.

*C. emini* (Günther; 1888a) was based on a snake in which the ventrals lacked lateral keels, such individuals being not at all uncommon. Witte (1933m) recorded both *irregularis* and *emini* from Elisabethville, Kikondja, Lulenga, Nyonga, Shangugu without it apparently occurring to him that they were synonymous. The actual credit for synonymizing *emini* with *irregularis* goes to Flower (1933) who remarks that in Sudanese snakes the keels "on the ventral shields may be perceptible, just perceptible, or not perceptible." The question arises as to whether keels are always present in western, or distinct from central, African *irregularis*.

*C. vernayi* FitzSimons (1932), was synonymized by Bogert (1940) with *irregularis* in the broad sense in which it was then understood.

Sternfeld's (1908b) Togo record of "*natalensis*" was referred by Angel (1933f) to *irregularis*, but the data clearly suggests he was dealing with an example of *heterolepidotus*. I myself (1936h:

1937c) was mistaken, though with good reason, for considering that *heterolepidotus* (Günther) and *schubotzi* Sternfeld were synonyms of *irregularis* (Leach).

It may be observed that on the basis of scale-counts there are some slight grounds for separating a northwestern race of *irregularis* from those in the rest of Africa (for Angola and Congo snakes are essentially like those extending towards the southeast). The actual figures are:

*Subcaudals*

Southeast etc. ♂ ♂ 103 (Angola) and 106 (Nyasaland) to 121 (Nyasaland).

Northwest ♂ ♂ 113 (Liberia) to 127 (Sierra Leone).

Southeast etc. ♀ ♀ ? 90 (Angola) and 97 (Nyasaland) to 121 (Angola).

Northwest ♀ ♀ 100 (Dakar) to 119 (Sierra Leone).

*Ventrals*

Southeast etc. ♂ ♂ 150 (Angola) and 152 (Nyasaland) to 167 (F. E. Africa).

Northwest ♂ ♂ 162 (Liberia) to 179 (Portuguese Guinea).

Southeast etc. ♀ ♀ 153 (Nyasaland), 154 (Angola) to 170 (Angola; Sudan).

Northwest ♀ ♀ 162 (Sierra Leone) to 183 (Senegal).

However, the overlap in *average* specimens is so extensive that an attempt at separation would inevitably result in deplorable confusion.

*Dentition.* Maxillary teeth 22 (Liberia) to 28 (Congo, etc.) in six snakes examined by Bogert (1940), who found that they were subequal in some, increasing in size posteriorly in others.

*Anatomy.* Parotids present (Phisalix).

*Hemipenis.* Not bifurcate; sulcus spermaticus undivided; basal spines large, merging on the middle third into reticulate calyces which grade into papillae towards the tip, which extends to the seventh or ninth subcaudal (Bogert).

*Sexual dimorphism.* None so far as the number of ventrals and subcaudals are concerned.

*Breeding.* At various times I have recorded the following: On September 30, a Misuku Mtns. ♀ held 11 eggs measuring *ca.* 15 x 11 mm.

October 9, a Misuku Mtns. ♀ held 7 eggs measuring *ca.* 30 x 12 mm.
December 21, a Bundibugyo ♀ held 5 eggs measuring *ca.* 22 x 7 mm.
December 28, a Chirinda Forest ♀ held 8 well-developed eggs (FitzSimons).
January 16, Ruwenzori Mtns. ♀ held 5 eggs from 28 x 12 to 32 x 11 mm.
February 10, a Kisenyi ♀ held 8 eggs measuring *ca.* 25 x 10 mm.

Also, on February 1, at Mushongero, Lake Mutanda, a native brought me 193 eggs, allegedly dug from two termitaria. One batch of 8 eggs measured 25 x 14 mm., another of 8 measured 39 x 17 mm., while 3 eggs selected from other batches measured 43 x 18 mm., 30 x 18 mm., and 29 x 18 mm. respectively, their diameter evidently conditioned by the girth of the parent. Each egg contained an embryo nearly ready for hatching, the embryo measuring 203 (143 + 60) mm., and on hatching a few weeks later a ♂ measured (180 + 80) mm., and a ♀ 249 (180 + 69) mm.

*Diet.* I have recorded a large lizard (*Lacerta jacksoni*), toads (*Bufo r. regularis*) twice, as also FitzSimons. Mertens has reported a tree-frog (*Leptopelis* sp.?) in one stomach and Laurent recovered sedge-frogs (*Hyperolius m. angolensis*) from two snakes. I found a sedge-frog (*Hyperolius schubotzi*) in each of three Idjwi Island *irregularis*, and an unidentifiable *Hyperolius* in a Nyasa snake; a frog (*Rana f. fuscigula*) at Lake Mutanda, and two *Rana o. oxyrhynchus* in Cholo reptiles.

*Parasites.* Hemogregarines were found in Stanleyville snakes by Schwetz; nematodes (*Amphicaecum* sp. and *Ascaroidea* sp.) in an Idjwi specimen (Loveridge).

*Enemies.* Two were recovered from the stomachs of vine-snakes (*Thelotornis k. kirtlandii*) on Cholo Mountain.

*Temperament.* A Kisenyi snake, when suddenly seized, gaped until its jaws were almost in a single plane; then it struck, the teeth drawing a little blood (Loveridge).

*Habitat.* Occurs from sea-level to 7,000 feet, having been taken in Belgian Ruanda just below the Bihunga Escarpment (Bogert). In the Sudan it has been found in an outhouse and beneath a rock on a mountain top (Corkill). In Uganda, it was captured

while basking on the bank of a dry watercourse at 6,000 feet, also among vegetation on the bank of the Amaler River at 5,000 feet. In fact it is generally associated with rivers, lakes, and swamps where its principal prey is to be found, though it also occurs in virgin forest (Loveridge). It has been recorded as present in borassus palm "forest" (Cott), in pawpaw tree (Schmidt), in papyrus (Stuhlmann), and the sudd. And it has been suggested that Khartoum records are due to these snakes having been transported there with agricultural produce carried on Nile steamers (Flower).

*Localities.* **Sudan:** Bahr el Jebel; Hellet Nuer; *Kagelu; *Katire; Lake No; Metemma; *Mongalla; Moro; Talodi. **Ethiopia:** *Mtemma (on Sudan frontier: C.N.H.M. 12719). **Uganda:** Bihunga Escarpment; *Bukatakata; *Bundibugyo; *Bussu (an intermediate); *Debasien Mtn.; Entebbe; Fort Portal; *Gulu, Aeholi; Kabulamuliro; Kampala; Katonga River; Katunguru, Kasinga Channel; Kayonza (Kanjonsa), Kagera River; Kayonza Forest; Kigezi; Kishasha Valley; *Kissolo; Komo Id.—*Busiro; Kyagwe Coast; Lado = West Nile District; Lake Albert; *Lake Bunyonyi; Lake Chahafi; Lake Edward; Lake George; *Lake Mutanda—*Mushongero; Lake Nakwali, Ankole; *Lira, Lango; Lugazi, Kyagwe; *Mabira Forest—*Mubango; Masaka; Nkosi Id.; Rhino Camp, Lado; *Ruwenzori Mts.—Kilembe, *Mihunga Ridge, Mubuku Valley; Wadelai. **Tanganyika Territory:** Bukoba; Bwanja near Bukoba; *Kibondo; *Kihambwe River, Kibondo; *Matengo Mts., *Nyarunga, Kibondo; *Mwaya; Rungwe Mtn.; Tukuyu (as Langenburg); *Ugano. **Mozambique.** Boror (Praso Boror); Charre; Fambani; Quilimane (type of *güntheri*). **Nyasaland:** *Blantyre (type of *shirana*); *Chiradzulu Mtn.; *Cholo Mtn.; Fort Hill; Karonga to Kondowe; *Limbe; *Misuku Mts.; Mlanje Mtn.; *Mtimbuka; *Nchenachena; "Nyika Plateau" (1897e); *Ruo River; Shire Highlands and Valley. **Northern Rhodesia:** Kazungulu; Lealui (Lialui); Mumbwa; Upper Zambezi. **Southern Rhodesia:** Chirinda Forest; *Chishawasha; Mashonaland; Mazoe[93]; Salisbury[93]; Selinda Mtn.; Selukwe; Umtali; Victoria Falls. **Bechuanaland Protectorate:** Maun (type of *vernayi*). **Southwest Africa:** Damaraland (1887h;

[93] Labial arrangement checked by Walter Rose; cf. footnote to Salisbury example of *hoplogaster*.

1894a); Otjimbingue (Peters:1867b). **Angola** (inc. *angolensis* records): *Bella Vista; Bimbi; *Caconda; Cambondo; Capelongo; Cazengo region; Chingo; Congulu; Cuango; Cubal; Cubango; *Cuma; *Cunga; Dundo; Duque de Braganca; Loeti River (as *neglectus*); Malange; Moco Mtn.; Mossamedes; Muita; Mupa; Mutianvo; Ndala (Ndallo) Tando; Pungo Ndongo; Rio Mbale; San Salvador; Vila da Ponte. **Cabinda:** Chinchoxo; Landana. **Belgian Congo:**[94] Aba; Albertville; Beni; Bishakishaki River; Bobandana; Boma; Bulengo near Lake Mugunga; Burunga; Buye-Bale River; Dika; Dramba; Elisabethville; Faradje; Ganza; Ishango, Semliki River; Idjwi Id.—*Upper Mulinga River; Kabenga; Kabengere; Kabwe; Kakyelo; Kalondo, Mokoto; Kalule-Nord River; Kamalondo Plain; Kando; Kankunda River; Kansenia; Kantana, Lake Kivu; Kanzenze; Kapanga; Kapiri; Kasenga; Kaswabilenga; Katanda, Lake Ndaraga; Katobwe; Kenia; Kikondja; Kilwa; Kilwezi; Kisala; Lake Tanganyika; Lukafu; Lukoka River; Lukolela; Lukonzolwa; Lukuga River; Lululabourg; Lusinga; Mabwe; Mahagi Port; Makaia Ntete; Makala; *Mangbetu (Monbuttu: type of *emini*); Masombwe; Mati; *Mayumbe; Mokabe-Kasari; Mpala; Mubale-Munte; Mukandwe; Mulungu; Mulungwe River; Munagana, Lake Rukuru; Mutwanga; Ngesho; Niangara; Nyangwe; Nyonga; Nyunzu; Panda; Pare Upemba; Pelenge; Povo Nemlao; Povo Netonna; Pweto; Rungu; Rwindi; Sake, Lake Kivu; Sandoa; Savane; Stanleyville; Tshishaka; Tshumba; Upper Uele River; Vista; Yakululu; Zambi; Zongo. **Belgian Ruanda-Urundi:**[94] Below Bihunga Escarpment; Goma, Lake Kivu; Kalondo, Lake Ndaraga; *Kisenyi, Lake Kivu; Lulenga: Rwankeri: Shangugu, Lake Kivu; Usumbura. **French Congo:** Abiras; Gabon; Yakoma. **French Equatorial Africa:** *Fort Crampel: *Fort Sibut. **French Cameroon:** Cameroon (type of *longifrenatus*); Bipindi; Satsche (not found on map); Tibati; Yaunde. **British Cameroon:** Kaka region, Bamenda District. **Nigeria:** Brass, Lower Niger River; *Ibadan; Owerri Province. **Togo:** Adele (as Bismarckburg); Atakpame; Kete; Moba; Yendi. **Ghana:** *Accra; *Achimota; *Adjiko, Krobo; Akropong; *Banda Hills; Christian Village; Fantee (type of *irregularis*). **Ivory Coast:**

[94] To these should be added 40 fresh localities: in the Belgian Congo (8), Ruanda (20) and Urundi (12) recently recorded by Laurent (1956, pp. 161-163).

Abidjan; Guiglo-Tai. **Liberia:** *Bolahun; *Ganta; *Gbanga; *Suacoco. **Sierra Leone:** *Bonthe; *Makeni; *Njala. **French Guinea:** "Guinea" (type of *chenonii*); Beyla; Dixine; Ferkessedougou; Kerouane; Labe, Fouta Djalon; Nimba Mtn.; Timbo; Ziela. **Portuguese Guinea:** *Bissau; Bolama; Caita; Pitche; Ponte. **Gambia:** *Cape St. Mary; *MeCarthy Id. **Senegal:** Bel Air; Canbarene Road near Dakar; Cap Vert (type of *caesius*); Dakar; Hann; Kati near Bamakko; Mbao; Rufisque; Sangalkam; Yoff. **French West Africa:** Dano near Diebougou, Upper Volta; Duong-Huu-Thoi; Kayo.

*Range.* Senegal, due east to Metemma (if data reliable), Ethiopia on Sudan border, on the White Nile, Sudan, south down Lakes Victoria, Tanganyika and Nyasa to Southern Rhodesia, west to Damaraland (single record), north and west to Senegal. In brief: West and Central Africa south of 15° N. and north of 20° S., but following the Zambezi east to the vicinity of Nyasaland.

### Philothamnus natalensis (Smith)

1840. *Dendrophis* (*Philothamnus*) *natalensis* A. Smith, Ill. Zool. S. Africa, Rept., pl. lxiv, figs. 1-3: "Port Natal," i.e. Durban, Natal, South Africa.
1847. *Dendrophis natalensis* Bianconi, p. 278.
1859. Bianconi, p. 502.
1858c. *Ahaetulla irregularis* var. *natalensis* Günther, p. 152.
1863c. *Ahaetulla natalensis* Günther, p. 285.
1890. Müller, p. 694.
1867a. *Leptophis irregularis* Steindachner (not Leach), p. 71.
1882c. *Philothamnus natalensis* Bocage, p. 18.
1884a. Rochebrune, p. 173 (omitted as erroneous).
1887b. Boettger, p. 160.
1887h. Boulenger (part), p. 176 (omit Damaraland).
1951c. Loveridge, pp. 4, 9.
1894a. *Chlorophis natalensis* Boulenger (part), p. 95 (omit Damaraland).
1898. Werner, 1896-7, p. 144.
1898. Sclater, p. 99.
1908b. Boulenger, p. 228.
1908. Gough, p. 24.
1908. Odhner, p. 5.
1910b. Boulenger (part), p. 507 (omit Kafue River).

1910a. Hewitt, p. 57.
1912. FitzSimons, F. W., p. 87.
1913. Hewitt & Power, p. 162.
1914a. Hewitt, pp. 242, 245, 246.
1929a. Werner, p. 100.
1935. Power, p. 334.
1937a. FitzSimons, V. F., p. 262.
1937e. Hewitt, p. 59, fig. 6.
1950. Fantham & Porter, p. 601.
1950. Rose, p. 271.
1955. Rose, pp. 92, 97.
1903. *Chlorophis angolensis* Gough (not Bocage), p. 465 (Durban).

Further citations of "*natalensis*" will be found under *hoplogaster, i. irregularis* and *heterolepidotus*.

*Common Name.* Natal Green-Snake (F. W. FitzSimons).

*Description.* Preocular 1; postoculars 2; temporals 2 + 2, rarely 1 + 2[95] or 2 + 1; upper labials 8-9, the fourth and fifth, or fifth and sixth, entering the orbit; lower labials 10-11, the first 5 in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 150-168[96] (♂♂ 150-165; ♀♀ 151-168); anal divided, rarely entire[97]; subcaudals 114-128 (♀♀ 114-122; ♂♂ 120-128).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above, olive green, the interstitial skin black; usually some scales with a white spot on their outer border. Below, chin and throat white, otherwise greenish white to pale green.

*Size.* Length of ♂ (B.M. 87.12.6.9) 775 (500 + 275) mm.; length of ♀ (B.M. coll. Stratham) 1083+ (755 + 328+) mm.

*Remarks.* The type of *natalensis* is not in the British Museum, and the specimen in the Royal Scottish Museum differs from Smith's description both in its fused temporals and greater dimensions (V. FitzSimons). The numerous subcaudals of *natalensis*, surpassed only by *heterolepidotus* and *semivariegatus*

[95] 1 + 2 of Boulenger (1894a :95) was based on the Kingwilliamstown specimen and has been checked.

[96] Actually 167 and 168 for the two Kingwilliamstown ♀♀ that Boulenger (1894a :95) recorded as 169.

[97] Entire only in a Natal ♂ (H. Calloway coll.) in the British Museum.

(*sensu lato*), with a trifling overlap by *i. irregularis*, and possibly the almost constant temporal arrangement of 2 + 2, suggest that *natalensis* is one of the most highly specialized members of the subgenus *Chlorophis*.

*Sexual dimorphism.* In ♀ ♀ the subcaudals range from 114 to 122; the ventrals overlap. In ♂ ♂ the subcaudals range from 120 to 128.

*Diet.* Sir A. Smith's statement that *natalensis* reputedly feeds on birds and insects may be discounted until established by concrete observations. A gecko (*Afroedura p. pondolica*) is present in the stomach of one Museum of Comparative Zoology specimen.

*Parasites.* To this species Fantham and Porter (1950) attribute the entozoa (*Entrichomastix serpentis*), and juvenile cysticerci that they found in the mucous and serous coats of the stomach, or embedded in the peritoneum, of a "3½ foot" ♂ and "4½ foot" ♀. If their measurements are correct, however, it would seem more probable that the snakes involved were *P. s. semivariegatus*.

*Habitat.* Shrubs and trees in the vicinity of Durban, where, being a good climber, the Natal Green-Snake is rarely seen on the ground (A. Smith).

*Localities.*[98] **Transvaal:** Henops River near Pretoria; Lydenburg; Middleburg; Pretoria; *Selati, Zoutpansberg District; Vryheid. **Natal:** Cathkin Peak, Drakensberg Mountains (V. Fitz-Simons coll.:1943); Caversham; Dargle Road; Durban; *Natal (head in M.C.Z.). **Cape Province:** Blue Cliff; Clarkesbury; Dunbrody; East London; Grahamstown; Harrismith; Kimberly; *Kingwilliamstown; Mossel Bay; Mqanduli; *Orange River; Port Elizabeth; *Port St. Johns; Tsomo.

*Range*[98]: Transvaal, south to Natal and eastern Cape Province.

### Philothamnus heterolepidotus (Günther)

1863e. *Ahaetulla heterolepidota* Günther, Ann. Mag. Nat. Hist., (3) **11**, p. 286: Africa.

1872a. Günther, p. 26.

1866a. *Leptophis heterolepidota* Bocage, p. 48.

1866b. Bocage, p. 69.

[98] The two Rhodesian specimens, i.e. Kafue River (Boulenger:1910b) and Salisbury (Boulenger:1902b), are assumed to be *hoplogaster;* the Damaraland snake proved to be an aberrant *i. irregularis*.

1879a. *Philothamnus heterolepidotus* Bocage, p. 96.
1882c. Bocage, p. 8, fig. 2.
1887a. Bocage, p. 185.
1888a. Boettger, p. 60.
1893. Pfeffer, p. 82 (possibly *semivariegatus*).
1895a. Bocage, p. 88.
1896a. Bocage, p. 100 (repeats Pfeffer's record for Mozambique).
1951c. Loveridge, pp. 5, 10.
1952. Witte, p. 19.
1953. Witte, p. 186, fig. 53.
1954b. Laurent, p. 48.
1954d. Laurent, pp. 292, 305.
1956. Laurent, p. 167, fig. 28, pl. xviii, fig. 2.
1888b. *Ahaetulla gracillima* Günther, Ann. Mag. Nat. Hist., (6) 1, p. 326: Lower Congo, Belgian Congo.
1894a. *Chlorophis emini* Boulenger (part:not of Günther), p. 92 (omit type from Monbuttu).
1903b. Andersson, p. 3.
1908a. Werner, p. 170.
1916a. Loveridge, pp. 78, 83, 84.
1918a. Loveridge, p. 333.
1924b. Loveridge, p. 5.
1929h. Loveridge, p. 21.
1933m. Witte (part), p. 88.
1935a. Corkill (part), p. 16.
1951. Monard, p. 150.
1894a. *Chlorophis heterolepidotus* Boulenger, pp. 95, 358, pl. v, fig. 3.
1896d. Boulenger, p. 631.
1896. Tornier, p. 69.
1897b. Boulenger, p. 278.
1897. Tornier, p. 69 (reprint of 1896).
1897b. Tornier, p. 65.
1898. Boettger, p. 58.
1902a. Werner (part), p. 344 (part *irregularis*).
1905c. Boulenger, p. 112.
1908b. Sternfeld, pp. 214, 230.
1909a. Sternfeld, p. 14.
1910a. Sternfeld, p. 18 (perhaps omit Pfeffer's Quilimane record).
1912c. Sternfeld, p. 270.
1915a. Boulenger, p. 205.
1915c. Boulenger, p. 623.
1917. Sternfeld, p. 468.
1918a. Loveridge, p. 333.

1919a. Boulenger, p. 281.
1923. Schmidt, p. 76.
1924b. Loveridge, p. 5.
1926a. Mertens, p. 153.
1929. Hecht, pp. 333, 334.
1929h. Loveridge, p. 23.
1929a. Werner, p. 100.
1931. Monard, p. 104.
1932a. Parker, p. 219.
1933f. Angel, p. 106, figs. 39-39a.
1933m. Witte (part), p. 89.
1934. Pitman, p. 294 (but *heterolepidotus* is unknown from Rhodesia).
1934a. Schwetz, p. 380.
1936. Pitman, p. 277, pl. v, fig. 4; pl. E, fig. 2.
1937b. Monard, pp. 114, 120.
1938a. Pitman, p. 306.
1938b. Pitman, pp. 39, 90, 91, 306 (pls. as in 1936).
1940b. Monard, p. 175 (though possibly *irregularis*).
1942e. Loveridge, p. 273.
1950. Ionides, p. 101.
1950f. Laurent, p. 128.
1895. *Chlorophis gracillimus* Günther, p. 528.
1908b. *Chlorophis natalensis* Sternfeld (not A. Smith), pp. 214, 229.
1909a. Sternfeld, p. 14.
1910d. *Chlorophis gracilis* Sternfeld, Mitt. Zool. Mus. Berlin, **5**, p. 64: Dodo, French Cameroon.
1929. Hecht, p. 332.
1951. Monard, p. 150.
1912c. *Chlorophis schubotzi* Sternfeld, Wiss. Ergebn. Deut.-Zent.-Afrika-Exped. 1907-1908, **4**, p. 269, fig. 4: Bwanja, near Bukoba, Tanganyika Territory.
1915c. Boulenger, p. 622.
1924b. Loveridge, p. 5.
1929. Hecht, p. 332.
1929a. Werner, p. 100.
1916a. *Chlorophis irregularis* Loveridge (not Leach), p. 84.
1918a. Loveridge, p. 333.
1919d. Chabanaud, p. 567.
1924b. Loveridge, p. 5.
1929h. Loveridge, p. 23.
1935a. Corkill (part), p. 16.
1936j. Loveridge (part), p. 247 (omit Mt. Debasien).

1937c. Loveridge (part), p. 273 (omit Fort Sibut).
1941. Witte (part), p. 188 (Kalinga specimen).
1923. *Chlorophis bequaerti* Schmidt (part), Bull. Am. Mus. Nat. Hist., **49**, p. 75, fig. 3: Niangara, Belgian Congo (based on an aberrant *heterolepidotus* ♂ with entire anal; omit paratype ♀, which is regarded as a similar aberrant *irregularis*).
1933m. *Chlorophis ornatus* Witte (not Bocage), p. 88.
1933m. *Chlorophis hoplogaster* Witte (part:not Günther), p. 88 (Faradje).

Further citations of "*heterolepidotus*" will be found under *i. irregularis*.

*Common Names.* Slender Green-Snake (Loveridge); Strange-scaled Green-Snake (Pitman); *calumberembe* (Angola:Bocage); *chilembe* (Cabinda:Bocage); *lolengue-lengua* (Angola:Bocage).

*Description.* Preocular 1, rarely 2[99]; postoculars 2, rarely 1[100]; temporals 1 + 1, rarely 0 + 1[101] or 1 + 2; upper labials 7-9, the third and fourth,[101] or third, fourth and fifth, normally the fourth, fifth and sixth, entering the orbit; lower labials 9-11,[102] the first four, five, or six in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 164-193[103] (♂ ♂ 164-193; ♀ ♀ 169-193); anal divided rarely entire[104]; sub-caudals 109-134 (♀ ♀ 109-126; ♂ ♂ 115-134[105]).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above, dark or bronzy green, the interstitial skin black; some scales with a white basal spot. Below, chin and throat white, otherwise greenish white or yellowish to very pale green.

[99] Two present in a Kaimosi ♀ (M.C.Z. 29426).

[100] On both sides of a Kaimosi ♂ (M.C.Z. 29423).

[101] 0 + 1 through fusion with sixth labial on right side of a Tembwe ♀ (Mus. Congo 4184) whose fourth and fifth labials are also fused on this side, resulting in its determination as "*ornatus*" (Witte).

[102] Actually 12 on left side of a Poli ♀ (M.C.Z. 44104) resulting in the first seven labials being in contact with anterior sublingual.

[103] 193 in a Niangara ♂ (A.M.N.H. 12087).

[104] Entire in the holotype ♂ *bequaerti* (A.M.N.H. 12080) from Niangara.

[105] 134 in the type of *bequaerti*, besides a Lagos ♂ (B.M. 71.4.21.4) and a Katobwe snake (C.N.H.M. 12874). Laurent (1954b) gives 144 for a Dundo ♂, a figure which far surpasses all species except *semivariegatus*.

*Size.* Length of ♂ (M.C.Z. 48300) 730 (492 + 238) mm., from Kitaya, is exceeded by a ♂ (Laurent:1956) 745 (475 + 270) mm., from Makungu.

♀ (type of *heterolepidotus*) 662 (450 + 212) mm., remeasured.
♀ (type of *gracillimus*) 722 (480 + 242) mm., remeasured.
♂ (type of *bequaerti*) 652 (440 + 212) mm.
(type of *schubotzi*) 565 (380 + 185) mm.
(type of *gracilis*) 450 (300 + 150) mm.

*Remarks.* The type of *Ahaetulla heterolepidota* was stated by Günther (1863c) to have 187 ventrals and 125 subcaudals; amended by Boulenger (1894a) to 182 ventrals and 117 subcaudals recounted by Battersby and myself as 182 + 4 halves and 119 subcaudals while I find the former length of 441 + 216 mm. is now 450 + 212 mm. I mention this as the British Museum has a "Zanzibar Coast" specimen of almost identical proportions (423 + 215 mm.) and scale-counts as given by Günther for the holotype of *heterolepidota.* However, Mr. Battersby does not think that a transposition has taken place as the head scales of the Zanzibar snake do not tally with Günther's description.

*A. gracillima* Günther was referred to the synonymy by Pfeffer (1893); *C. gracilis* Sternfeld by Boulenger (1919a), whose "*emini*" was a composite of *heterolepidotus* + *emini* Günther, which is a synonym of *irregularis.* It was in this composite sense of "*emini*" that I (1936h) synonymized *C. schubotzi* Sternfeld with "*irregularis.*" In reality *schubotzi* is a synonym of *heterolepidotus* as here understood. To that synonymy I now add the ♂ type of *bequaerti* Schmidt which differs from typical *heterolepidotus* only in having an entire anal. The ♀ paratype of *bequaerti* I consider to be an aberrant *irregularis* with entire anal. Normal examples of both *heterolepidotus* and *irregularis* from Niangara were present in the same collection.

*Sexual dimorphism.* Unless there exists some slightly lower average subcaudal count for ♀ ♀, no other characters for separation of the sexes have been detected.

*Diet.* A sedge-frog (*Hyperolius cinnamomeoventris*) removed from a Makungu snake (Laurent:1956), others (*Hyperolius rossi* = *pachyderma*) and sp. were recovered from the stomachs of three Uganda snakes, also a frog (non det.) in a Tanganyika specimen (Loveridge:1942e).

*Habitat.* Apparently associated with tropical rain-forest or the gallery forests fringing the equatorial river systems.

*Localities.* **Sudan:** Barboi; Khartoum (probably introduced on Nile steamer); 500 miles south of Khartoum; *Torit; White Nile (1882). **Uganda:** *Bukatakata; Katunguru; *Lira, Lango; *Nyakabande; Rhino Camp, 2°55′, West Nile Province. **Kenya Colony:** *Kaimosi; *Kakamega; *Yala River. **Tanganyika Territory:** Bwanja near Bukoba (type of *schubotzi*); *Kibondo; *Kigoma; *Kitaya; Masailand (*fide* Sternfeld:1910a); a questionable record possibly based on a specimen of *semivariegatus*); *Nyarunga, Kibondo; Zanzibar coast (i.e. mainland opposite island). ? **Mozambique** (the sole record is that of Pfeffer (1893), repeated by Sternfeld (1910a), for three snakes from Njama Kette near Quilimane, possibly *semivariegatus*). **Angola:** Bihe; Bimbi; Caconda; Casangue; Catengue; Cuango (Quango); Cuibula (Quibula); Dundo (Dondo); Duque de Braganea; Kutatu (Kutato); Muita River; Sao Salvador. **Cabinda:** Cabinda (1895a). **Belgian Congo:**[106] Albertville; Boma; Cap Kasembondo, Lake Tanganyika; Duma; Elisabethville; Faradje; Inkangala; Kabongo; Kabwe; Kabwekanono Lake; Kadia; Kando[107]; Kapanga; *Katobwe; Kikondja; Landana; Lofoi; *Lower Congo (type of *gracillima*); Mahagi Port; Masombwe; Mubale-Munte; Musosa; *Niangara; Nyonga; Pweto; Tembwe; Tshikapar; Sandoa; Stanleyville; Zambi. **Belgian Ruanda-Urundi:**[106] Lake Kivu. **French Cameroon:** Dodo (type of *gracilis*); Kribi. **British Cameroon:** *Poli near Garoua. **Nigeria:** *Lagos. **Dahomey:** Porto Novo. **Togo:** Kete.

*Range.* Sudan from the Upper Nile southeast to the mouth of the Rovuma River, Tanganyika Territory (? Mozambique), west to Angola and north to Togo.[108]

### Philothamnus semivariegatus semivariegatus (Smith)

1847. *Dendrophis* (*Philothamnus*) *semivariegata* A. Smith, Ill. Zool. S. Africa, pls. lix, lx, lxiv, figs. 1a-b; Bushman Flat, Cape Province

[106] To these should be added 13 fresh localities: in the Belgian Congo (6), Ruanda (6) and Urundi (1) recently recorded by Laurent (1956, pp. 167-168).

[107] The Kansenia record is transferred to *i. irregularis*.

[108] Monard's (1940b) records from Portugese Guinea — 1300 miles west of Togo — appear to be based on examples of *i. irregularis*.

(restricted Bogert:1940) "and the country beyond Kurrichaine," i.e. Rustenberg, Transvaal.

1863e. *Ahaetulla semivariegata* Günther, p. 285.
1866b. *Philothamnus punctatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 889: Zanzibar Coast, i.e. Tanganyika Territory.
1869a. Peters, p. 16, pl. i, figs. 2a-e.
1878a. Peters, p. 206.
1882a. Bocage, p. 289.
1882c. Bocage, p. 14.
1882a. Peters, p. 129, pl. xixA, fig. 1.
1884a. Rochebrune, p. 173 (omitted as unreliable).
1889. Boettger, pp. 289, 294.
1893. Pfeffer, p. 83.
1896a. Bocage, p. 92.
1867a. *Leptophis* sp. Bocage, p. 226.
1868a. *Ahaetulla Kirkii* Günther, Ann. Mag. Nat. Hist., (4) **1**, p. 424: Zanzibar.
1869b. Günther, p. 116.
1869. *Dendrophis melanostigma* Jan. Icon. Gén. Ophidiens, No. 32, pl. ii, fig. 3: Mozambique.
1869b. *Philothamnus semivariegatus* Peters, p. 661.
1870b. Peters, p. 114.
1884a. Rochebrune, p. 173 (omitted).
1891a. Boulenger, p. 307.
1891b. Matschie, p. 615.
1893b. Stejneger, p. 728.
1894a. Boulenger, p. 99.
1895a. Bocage, p. 90, pl. xiii, figs. 2a-c
1895c. Bocage, p. 13.
1895. Jeude, p. 229.
1896a. Bocage, pp. 78, 83.
1896b. Bocage, p. 112.
1896d. Boulenger, p. 631.
1896e. Boulenger, p. 216.
1896. Tornier, p. 70.
1897. Bateman, p. 268.
1897b. Boulenger, p. 278.
1897d. Boulenger, p. 375.
1897e. Boulenger, p. 801.
1897g. Boulenger, p. 279.
1897i. Boulenger, p. 20.

1897. Meek, p. 179.
1897. Tornier, p. 65.
1898. Boettger, p. 58.
1898a. Boulenger, p. 720.
1898. Ferreira, p. 244.
1898. Johnston, p. 361a.
1898. Sclater, p. 99.
1898. Werner, 1896-7, p. 144.
1899a. Mocquard, p. 219.
1900b. Boulenger, p. 452.
1901. Schenkel, p. 160.
1902a. Boulenger, p. 446.
1902b. Boulenger, p. 17.
1902a. Werner, pp. 339, 344.
1903b. Andersson, p. 3.
1903a. Bocage, p. 43.
1907a. Boulenger, p. 10.
1907j. Boulenger, p. 486.
1907. Lönnberg, p. 15.
1907a. Roux, p. 76.
1907c. Roux, p. 735.
1908b. Boulenger, p. 229.
1908. Gough, p. 24.
1908b. Mocquard, p. 558.
1908. Odhner, p. 5.
1908b. Sternfeld, pp. 214, 230.
1908c. Sternfeld, pp. 243, 246.
1908. Werner (1907), p. 1873.
1909d. Boulenger, p. 311.
1909a. Sternfeld, p. 15.
1910b. Boulenger, p. 508.
1910a. Sternfeld, p. 19.
1910b. Sternfeld, p. 19, fig. 19.
1910c. Sternfeld, p. 55.
1911c. Boulenger, p. 165.
1911. Lampe, p. 193.
1911b. Nieden, p. 442.
1911a. Sternfeld, p. 250.
1912b. Boulenger, p. 332.
1912. FitzSimons, F. W., p. 87.
1912. Hobley, p. 49.
1912c. Sternfeld, p. 270.

1913. Boettger, pp. 345, 352, 359, 363.
1913. Hewitt & Power, p. 162.
1913. Klaptocz, p. 285.
1913. Lönnberg & Andersson, p. 4.
1913a. Werner, p. 373, pl. vii, fig. 2.
1913b. Werner, p. 717.
1915a. Boulenger, p. 206.
1915c. Boulenger, p. 623.
1915d. Boulenger, p. 648.
1916. Calabresi, p. 39.
1916f. Chabanaud, p. 372.
1916a. Loveridge, p. 84.
1917b. Chabanaud, p. 11.
1917a. Phisalix, p. 334.
1917. Sternfeld, p. 470.
1918a. Loveridge, p. 332.
1919a. Boulenger, p. 282.
1919g. Boulenger, p. 23.
1920. Aders, p. 338.
1921a. Chabanaud, p. 468.
1921b. Chabanaud, p. 524.
1921. Falk, p. 177.
1922. Aylmer, p. 15.
1922. Falk, p. 162, photo fig.
1923e. Loveridge, p. 879.
1924b. Loveridge, p. 5.
1925a. Angel, p. 33.
1925a. Loveridge, p. 72.
1927. Calabresi, p. 53.
1927c. Power, p. 409.
1928c. Barbour & Loveridge, p. 118.
1928. Cott, p. 953.
1928d. Loveridge, p. 53.
1928j. Loveridge, p. 74.
1929. Flower, p. 204.
1929h. Loveridge, p. 24.
1929e. Scortecci, p. 274.
1929a. Werner, p. 98.
1930a. Scortecci, p. 212.
1930e. Scortecci, p. 17.
1931. Monard, p. 104.
1931. Power, pp. 43, 48.

1931c. Scortecci, p. 206.
1932b. Scortecci, p. 45.
1933b. Angel, p. 69.
1933f. Angel, p. 110, figs. 40-40a.
1933. Schmidt, p. 13.
1933m. Witte, p. 89.
1934a. Schwetz, p. 381.
1935a. Corkill, p. 17.
1935. Cott, p. 967.
1935. Power, p. 334.
1937. Andersson, p. 8.
1937a. FitzSimons, V. F., p. 262.
1937c. Hewitt, p. 60, fig. 5, pl. xviii.
1937b. Monard, pp. 114, 122.
1938. FitzSimons, V. F., p. 156.
1939a. Scortecci, p. 274.
1940a. Scortecci, p. 131.
1945. Leeson, p. 1.
1947. Ionides, 1946, p. 70.
1948. Ionides, 1947, p. 10.
1949a. Parker, p. 57.
1950. Leeson, pp. 46-48, 66, 133, figs. 20-22, pl. v.
1950. Rose, pp. 272, 314, fig. 9.
1950b. Villiers, p. 82, figs. 100-101.
1951. Monard, pp. 150, 160.
1954. Blair & Graham, p. 286.
1955. Rose, pp. 94, 178, fig. 9.[109]
1881. *Philothamnus irregularis* var. Fischer, p. 229, pl. xiv, figs. 5-7.
1884a. Fischer, p. 11.
1882c. *Philothamnus Smithii* Bocage, Jorn. Sci. Lisboa, **9**, p. 12, fig. 5: Bissau, Portuguese Guinea (restricted A.L.) and Angola.
1884b. Sauvage, p. 201 (as *Philothalmus*).
1886. Dollo, p. 156.
1887a. Bocage, p. 196.
1885. *Ahaetulla* sp. Müller, p. 683.
1886. *Ahaetulla irregularis* Parenti & Picaglia (not Leach), p. 74.
1930b. Zavattari, p. 193.
1888. *Leptophis punctatus* Mocquard, p. 128.
1888b. *Ahaetulla Bocagii* Günther, Ann. Mag. Nat. Hist., (6) **1**, p. 326: Angola.

[109] Variously spelled *Philothamnus* (92, 97), *Pholothamnus* (95), and *Philothammus* (212).

1895. Günther, p. 528.
1889. *Philothamnus irregularis* Pfeffer (not Leach), p. 9.
1902. Ferreira, p. 232.
1893. *Philothamnus punctatus* var. *thomensis* Pfeffer (not Bocage), p. 84.
1893. *Philothamnus punctatus* var. *sansibaricus* Pfeffer, Jahrb. Hamburg. Wiss. Anst., **10**, p. 83: Zanzibar.
1894. *Ahaetulla punctata* Günther, p. 88.
1895. *Philothamnus Kirkii* Günther, p. 528.
1896. *Philothamnus variegatus* Peracca, p. 2 (lapsus).
1948a. Villiers, p. 203.
1896. *Philothamnus dorsalis* Tornier (not Bocage), p. 71.
1897. Tornier, p. 65.
1925. Angel, p. 32.
1933m. Witte (part), p. 90 (Faradje).
1896. *Philothamnus thomensis* Tornier (not Bocage), p. 71.
1897. Tornier, p. 65.
1910a. Sternfeld, p. 19.
1940. Parker, Moreau & Pakenham, p. 310 (correct earlier record).
1908c. *Chlorophis irregularis* Sternfeld (not Leach), p. 243.
1911. Lepri, 1910, p. 324.
1930a. Scortecci, p. 212.
1923. *Philothamnus nitidus* Schmidt (not Günther), p. 78 (intermediates).
1925a. Angel, p. 32.
1930a. Barbour & Loveridge, p. 772.
1930b. *Chlorophis emini* Zavattari (not Günther), p. 193.
1933h. *Philothamnus semivariegatus semivariegatus* Loveridge, p. 238.
1934e. Mertens, pp. 27, 83, 118, 119.
1934. Pitman, p. 295.
1935b. FitzSimons, V. F., p. 313.
1936h. Loveridge, p. 32.
1936j. Loveridge, p. 247.
1936. Pitman, p. 42, pl. vi, fig. 1; pl. D, fig. 3.
1937e. Loveridge, p. 273.
1937f. Loveridge, pp. 493, 496, 503.
1937a. Parker, pp. 630.
1937b. Mertens, p. 13.
1937. Uthmöller, p. 110.
1938e. Mertens, p. 439.
1938a. Pitman, pp. 307, 328.
1938b. Pitman, pp. 39, 97, 295, 307, 328, pls. (as in 1936).
1939b. FitzSimons, V. F., p. 22.
1940. Bogert, p. 56.
1941. Moreau & Pakenham, p. 108.

1941a. Uthmöller, pp. 26, 42.
1941b. Uthmöller, p. 235.
1941. Witte (part), p. 199 (Bugazia).
1942b. Bogert, p. 2.
1942e. Loveridge, p. 274.
1945b. Loveridge, p. 2.
1950. Ionides, p. 101.
1950f. Laurent, p. 126 (possibly some *P. s. dorsalis*).
1950a. Villiers, p. 61.
1951a. Loveridge, p. 192.
1951c. Loveridge, p. 11.
1952. Witte, p. 19.
1953e. Loveridge, pp. 262, 318, pl. iv, fig. 1.
1953. Witte, p. 195, fig. 56.
1954. Battersby, p. 247.
1954b. Laurent, p. 48.
1954d. Laurent, pp. 292, 305.
1955a. Mertens, p. 93.
1933h. *Philothamnus semivariegatus dorsalis* Loveridge (presumably not of Bocage, being 22 intermediates from Mwaya, Lake Nyasa; cf. remarks under *s. dorsalis*), p. 238.
1937f. Loveridge, p. 496.
1936. Pitman (part), p. 44.
1938a. Pitman, p. 307.
1938b. Pitman, pp. 99-100, 307.
1941. Witte, p. 200.
1946b. *Philothamnus* Mertens, pp. 17, 24 (defense reactions).
1954d. [110] *Philothamnus semivariegatus nitidus* Laurent (not Günther), p. 296.
1956. Laurent, p. 180.

Further citations of "*semivariegatus*" will be found under *i. battersbyi* and *s. nitidus*.

*Common Names.* Spotted Wood-Snake (Flower); sundry other names have been suggested by Pitman (1938b, p. 97). *Alakara guindé* (Habbe at Bandiagara: Angel); *changa* (Yao: Loveridge); *ekumbu* (Teita: Loveridge); *hasowitu* (Pokomo: Loveridge); *kada* (Dahomey: Bocage); *kalembwe-lembwe* (Dundo: Laurent); *kisumera* (Makonde at Kitaya: Loveridge); *kongoani* and *ukutiwiti* (Amu: Loveridge); *lubio* (Catumbela: Bocage);

[110] But data derived from 1956 reference not incorporated here for reasons given in footnote to *P. s. nitidus*.

*mlaluwe* (Hehe: Loveridge); *namafwa* (Fipa: Loveridge); *namahamba* (Konde at Mikindani: Loveridge); *nalwinduwindu* (Misuku: Loveridge); *nawirangira* (Mawiha: Loveridge); *nhanga* (Gogo: Loveridge); *nombo* (Benguela: Bocage); *nyarubabi* or *nyaruteti* (Toro: Loveridge); *nyoka masamba* (i.e. garden snake. Nyungwe: Loveridge); *ngoe* (Sambaa, but supposed to be the young of *D. angusticeps*: Loveridge); *salalu* (Amba: Loveridge); *yarudutu* (Nyamwezi: Loveridge).

*Description.* Preocular 1, rarely 2[111]; postoculars 2, rarely 1 or 3[112]; temporals usually 2 + 2, sometimes 1 + 1, 1 + 2, 2 + 1 or 2 + 3[113]; upper labials 8-10, the fourth and fifth; fourth, fifth and sixth; fifth and sixth; or rarely fifth, sixth and seventh entering the orbit[114]; lower labials 9-11, the first four, five or six in contact with the anterior sublinguals; midbody scale rows 15, rarely 13[115]; ventrals 164-217; anal divided; subcaudals 126-162.[116]

[111] Summary of preocular arrangement on 103 snakes in the M.C.Z.
102 have 1 preocular on each side of the head.
1 has 1 preocular on one side 2 on other (30138: Kigogo).

[112] Summary of postocular arrangement on 105 snakes.
1 has 1 postocular on each side of the head.
103 have 2 postoculars on each side of the head.
1 has 2 postoculars on one side 3 on other (40528: Debasien).

[113] Summary of temporal arrangement on 107 snakes.
1 has 1 + 1 on each side of the head (42169: Waterberg: *t.dorsalis*).
2 have 1 + 1 on one side of the head 1 + 2 on the other.
6 have 1 + 2 on each side of the head
6 have 1 + 2 on one side of the head 2 + 2 on the other.
2 have $\frac{1}{1} + \frac{1}{1}$ or $\frac{1}{1} + \frac{1}{1+1}$ on each side (23259: Vituri; & Eritrea).
5 have " or " on one side 2 + 2 on the other.
3 have 2 + 1 on each side of the head.
7 have 2 + 1 on one side of the head 2 + 2 on the other.
1 has 2 +1 on one side of the head 2 + 3 on the other.
74 have 2 + 2 on each side of the head.

[114] Summary of upper labial (entering orbit) arrangement on 112 snakes
1 has 8 (with 3rd only, due to fusion) on each side (M.C.Z. 54825).
2 have 8 (with 4th & 5th) on one side, 9 (with 5th & 6th) on other.
2 have 8 (with 4th & 5th) on one side, 9 (4th, 5th & 6th) on other.
1 has 8 (with 5th only) on one side, 9 (with 5th & 6th) on other.
39 have 9 (with 5th & 6th) on each side.
8 have 9 (with 5th & 6th) on one side, 9 (4th, 5th & 6th) on other.
1 has 9 (with 5th & 6th) on one side, 10 (with 5th & 6th) on other.
48 have 9 (4th, 5th & 6th) on each side.
1 has 9 (4th, 5th & 6th) on one side, 10 (4th, 5th & 6th) on other.
8 have 9 (4th, 5th & 6th) on one side, 10 (5th, 6th & 7th) on other.
1 has 10(5th, 6th & 7th) on one side, 10 (with 6th & 7th) on other.

[115] 13 in a Kibwezi ♂ (M.C.Z. 40530) : also reported by Pitman (1936, p. 328) for a Lake Albert specimen.

[116] 162 for an unsexed Belet Amin snake (*fide* Scortecci, 1939a), my highest is 161 for a Morogoro ♀ (M.C.Z. 18451), 160 for a Peccatoni ♂ (M.C.Z. 40538). Laurent (1950) has as low as 122 and 123 for Dundo ♀♀, 121 and 125 for Uvira and Lukuga ♀♀ (1956, p. 179); see latter for other data and discussion.

*Color.* Above, head and body anteriorly dark green, uniform, or with a series of brown or black crossbars on nape and anterior part of back; usually some scales display a turquoise blue, or white, streak either with, or without, black edging; posteriorly paler green, with or without black spots on flanks. Below, labials, chin and throat yellow or white; belly yellowish green to yellow; subcaudals pale green or yellow.

Laurent observes (1954b:48) that in a series of 5 ♂♂ and 4 ♀♀ from Dundo and vicinity, the underside was distinctly lighter than the back in the ♂♂, but ventral coloring did not differ from the dorsal in the ♀♀.

The coloring, however, is extremely variable and the literature should be consulted for countless comments. Leeson (1950, p. 48) has figured a Ghana snake in color. The striking appearance of four Mozambique snakes noted by me (1923e, p. 879) was as follows: Above, head and neck pale green; body mauve, both freely speckled with black; tail plumbeous. Below, throat china-white; rest of undersurface whitish tinged with mauve, the ventral keels distinctly mauve. Tongue light blue, except for the tip and root which were black. Apparently these variations are not static enough to form a sound basis for geographical races. For example at Kitaya, on the Rovuma River, snakes with both blue and green heads were present, but at nearby Mikindani only one of a series of six *semivariegatus* had a blue head.

Pitman has described the eye of a freshly killed snake as having the pupil large, circular, black; iris ring narrow, golden or deep yellow. Bocage's type was said to have deep reddish-brown eyes, the pupils surrounded with a narrow silvery ring. The tongue has been described as blue-green anteriorly, black at the tip and base (Falk:1922).

*Size.* Length of ♂ M.C.Z. 30137) 1205+ (800 + 405+) mm., from Mangasini; a perfect ♂ (M.C.Z. 30133) 1174 (742 + 432) mm., from Bagamoyo; length of ♀ (M.C.Z. 40534) 1233 (785 + 448) mm., from Lamu Id.

*Remarks.* Measurements are the only information furnished by Parenti and Picaglia (1886) for the "*Ahaetulla irregularis*" they recorded from Assab, Eritrea. Whatever the species, much of the tail would appear to be missing for they give the length as 820 (630 + 190) mm. A ♀ *i. battersbyi* from Mabira Forest

with a 627 mm. body has a 253 mm. tail; a ♂ *s. semivariegatus* from Mikindani with 620 mm. body has a 366 mm. tail; a ♀ *s. semivariegatus* from Siga Caves has 630 mm. body and a 350 mm. tail. As *P. irregularis* is unknown from Eritrea (apart from this oft-repeated record) and *P. s. semivariegatus* does occur there, I believe their snake was a misidentified *semivariegatus*. Similarly the "*irregularis*" from Mogadiscio, recorded by Lepri (1911) is clearly a *semivariegatus*, its length 917 (602 + 315) mm. of tail far exceeding that of any eastern *irregularis* (i.e. *battersbyi*).

Parker, Moreau and Pakenham (1940) comment on the Jambiani Id. snake that Pfeffer (1893) erroneously referred to *thomensis*. Boulenger (1907j) points out that the labial and temporal arrangements of a Beira snake agree with *semivariegatus* on one side and with *kirkii* on the other. Angel's (1933f) figures of 140-207 ventrals and 112-159 subcaudals are rejected as unacceptable; Pitman (1936) gives 149-207 and 112-159 respectively. FitzSimons (1937a) states that one of three snakes from Bushman Flat in the Royal Scottish Museum agrees precisely with the dimensions and subcaudal count of Sir A. Smith's type, but the ventrals are actually 215, not 207 as stated by Smith. A juvenile *nigrofasciatus* in the same museum resembles the specimen figured on Smith's plate lx.

*Dentition.* Maxillary teeth 21, subequal, but not so closely set as in "*Chlorophis*" (Bogert: 1940). Leeson (1950), who puts them at 14 to 20, usually 18, posterior longer than anterior, may not have allowed for shed teeth. He adds: palatine teeth 8; pterygoid 13; mandibular up to 26, subequal, or median teeth shorter than the others.

*Anatomy.* Parotids present (Phisalix).

*Sexual dimorphism.* The extensive material in the Museum of Comparative Zoology reveals that there is no sexual dimorphism in lepidosis; viz:

In ♂ ♂ the ventrals range from 164-217, the subcaudals 127-160.
In ♀ ♀ the ventrals range from 164-200, the subcaudals 126-161.

The extreme figures have been subjected to careful re-checking: all lower counts of subcaudals were found to have regenerated tail tips. It is possible that ♂ ♂ have relatively longer tails, a

point that requires investigation; in three Tanganyika ♀ ♀ Bogert found the ratio of tail length into total length was 32, 32, and 34%.

*Breeding.* The season is probably related to those of the monsoons, and not as extensive as the nine observations I have made would appear to suggest.

On October 14, in Matipa Forest, a ♀ held 5 eggs measuring 41 x 12 mm.

On November 25, at Morogoro, a ♀ held 6 eggs of small size.

On December 3, in Budongo Forest, a ♀ held 4 eggs measuring 30 x 8 mm.

On March 25, at Kitaya on Rovuma, a ♀ held 7 eggs measuring 21 x 7 mm.

On April 3, at Kitaya on Rovuma, a ♀ held 6 eggs measuring 11 x 3 mm.

On April 20, at Mikindani, a ♀ held 5 eggs measuring 28 x 8 mm.

On April 21, at Mikindani, a ♀ held 3 eggs measuring 29 x 8 mm.

On May 1, at Mbanja near Lindi, a ♀ held 5 eggs measuring 20 x 5 mm.

On May 5, at Mbanja near Lindi, a ♀ held 5 eggs measuring 24 x 6.5 mm.

On May 18, in the Bangweulu area, a ♀ held eggs, according to Pitman (1936) whose record, apart from my own, appears to be the only dated one in the literature.

*Diet.* Pitman (1934) remarks that "frogs form an important part of its diet," but I think this is so only when they are young. I have recovered only 7 amphibia (*Bufo r. regularis; Leptopelis concolor; Megalixalus brachyenemis* and *Hyperolius p. parkeri*) from 5 snakes, but more than 25 lizards, chiefly geckos (*Hemidactylus b. angulatus; H. mabouia; Lygodactylus g. grotei; L. p. gutturalis; L. p. ukerewensis; L. p. mombasicus* and *Ablepharus wahlbergii*) from a score of these wood-snakes; a skink (*Mabuya s. striata*) has also been found in one by K. P. Schmidt.

One wood-snake disgorged a gecko (*Pachydactylus b. turneri*) when captured, but so large a species is usually more than they can manage for I found two tails of adult Turner's geckos in another; the lizards themselves having managed to escape by detaching their caudal appendages.

*Parasites.* Nematodes (*Thubunaea* sp., probably *asymmetrica*) and immature cestodes were present in a Mikindani snake (A.L.).

*Enemies.* Ionides (1947) observed in the bill of a White-headed Black-chat (*Thamnolaea a. leucolaema*) a foot-long wood-snake which was dropped as he approached; however it succumbed to head injuries very shortly afterwards. I recovered a young one from the stomach of a One-streaked Hawk (*Kaupifalco monogrammicus*), and an adult from a Banded Harrier Eagle (*Circactus fasciolatus*).

*Defense.* Until molested, a Spotted Wood-Snake is apt to rely on its color and build, which, until it moves, usually render the reptile difficult to distinguish from surrounding twigs. At Kilosa I once approached a wood-snake engaged in swallowing a gecko. The predator promptly disgorged its prey and, as I seized its own tail, the snake filled its oesophagus with air so as to vertically distend the entire anterior portion of the body while it repeatedly struck at my hand. Similarly a fine male, captured alive at Chitala, inflated its throat vertically as its photograph was being taken (1953e, pl. iv, fig. 1). This intimidating behavior is shared with sundry other arboreal snakes (*Thrasops* spp., *Dispholidus typus* and *Thelotornis kirtlandii*).

*Habits.* The slender, lash-like tail is admirably adapted to an arboreal life. By its aid, and taking advantage of every irregularity in the bark, I once saw a wood-snake *ascending* the trunk of a great fig tree on Debasien Mountain. Similarly, my attention being attracted to the reptile by the outcries of some birds, I was able to observe at my leisure a bush-snake *descending* the almost vertical trunk of a tree at Frere Town. At Kitaya I shot a female with truncated tail as it was basking, draped about a knot-hole in the bole of an almost upright tree.

The prehensile qualities of this reptile's tail were demonstrated on another occasion when, in pursuit of a wood-snake I climbed one of the acacias forming part of the avenue leading to Government House, Morogoro. The snake quickly sought refuge in the topmost twigs. When I agitated these the snake flowed swiftly along the branches to the next acacia, in which my African assistant was already enseonced. When the limb on which the snake was travelling was shaken violently, the reptile wrapped itself tightly about the branch but was eventually shaken loose

and fell to the ground twenty feet below. On landing, without a moment's hesitation it made off. I intercepted its departure and was bitten a couple of times, the fine teeth drawing blood.[117] However, as Power has said, following the initial fright of capture, this species does not resent handling.

Once, in this same avenue, a bush-snake was found ensconced in the hood of a car parked beneath the acacias, and another time the violence of a blustering gale dislodged a bush-snake from a tree beneath which I happened to be standing.

In a flooded area I found a bush-snake in the company of a *P. i. battersbyi*, the two reptiles having taken refuge in a young doom palm; yet another was among the water plants in waist-deep water where it was presumably hunting frogs. Seemingly they hunt by night as well as by day, for once at 8 p.m.I captured a bush-snake on a spray of bramble when it was only a foot from a tree frog (*Chiromantis xerampelina*) that it was apparently stalking. The bush was growing in knee-deep water, no obstacle to a bush-snake for as Pitman has stated, the species "swims gracefully and with speed."

*Habitat.* Coastal plain, upland savanna, and montane forest-edge (Loveridge). Young ones were taken in heaps of stones beyond Kurrichane (A. Smith); apparently abundant in palm forest (Cott); living in coffee trees (Uthmöller) and a mango tree (Laurent).

*Localities.* **Arabia** (*fide* Scortecci:1932b): Yemen. **Sudan:** Bahr el Ghazel; Delami; Gondokoro; Khartoum; *Lake Nyibor; *Mongalla; *Torit. **Eritrea:** Assab (as *irregularis*); Gura. **Ethiopia** (*fide* Scortecci:1943). **British Somaliland:** Bohodle; Golis Mtns.; Haud; Sheikh; Wagar. **Somalia:** Afgoi; Afmadu; Bardera; Belet Amin; Comia to Matagoi; Dolo; Goscia; Kismayu; Lugh; Mada (Madu); Mahaddei Uen; Mofi; Mogadiscio; Villaggio Duca del Abruzzi. **Uganda:** *Abera; *Budongo Forest; Buhukya; *Bundibugyo; *Busingiro; Bussu; Butiaba; *Debasien Mtn.; Kaiso; *Katwe; Kome Id.; Lubwa's, Usoga (1896); Sesse Ids. **Kenya Colony:** *Bura; *Diani Beach; *Jilore; *Kibwezi; Kilibassi; Kurawa; *Lamu Id.; *Malindi; *Manda Id.; *Mbololo Mtn.; Mkonumbi; *Mombasa; *Murri; *Ngatana; *Peccatoni Lake; *Tana River; Teita; Voi. **Tanganyika Territory:**

[117] For effect of a bite on an Indian soldier, cf. Loveridge (1942g:120).

*Amboni Estate near Tanga; Arusha; *Bagamoyo; Dar es Salaam; Dunda; Gomberi; Ilonga; Kabare; *Karema; Kibongoto (Kibonoto); *Kigogo; Kilimanjaro Mtn.; *Kilosa; *Kilwa; *Kimamba; *Kipili; *Kitaya; Kizumbe; *Liwale; *Longido Mtn.; *Magrotto Mtn.; *Mangasini; *Manyoni; Masailand; *Matembo; Mavene near Tanga; Mawere Shamba; *Mbanja; *Mikindani; *Mombo; *Morogoro; Moshi; *Mwaya (intermediates); *Siga Caves; *Sigi; Tanga; *Tanganyika Lake; *Tindi; *Tunduru; *Ugogo; *Ukerewe Id.; *Ulambo; Uluguru Mtns.—*Vituri; Usambara Mtns.—*Amani, Lewa; *Ujiji; Zanzibar Coast. **Pemba Id.:** *Mangapwami; *Verani; *Wete. **Zanzibar Id.:** Jambiani Id.; Kokotoni; Pete; *Zanzibar. **Mafia Id.: Mozambique:** Angoche; Beira; Boro; Cabaceira; Charre; Chifumbazi; Delagoa Bay; Fambani; Inhaminga; *Kasumbadedza; Lukungui; *Lumbo; Mgaza; Mozambique; Quelimane; Querimba Id.; Sofala. **Nyasaland:** Blantyre; *Chitala River; Fort Hill; Karonga to Kondowe; *Likabula River; *Misuku Mtns.; Nyasa Lake; "Nyika Plateau" (Boulenger 1897e); Shire River; Shire Valley. **Northern Rhodesia:** Broken Hill; Kazungula; Livingstone; Luangwa River in Serenje District; Mpika; Petauke; Swamps near Lake Bangweulu; Zambezi Plains. **Southern Rhodesia:** Devuli River Bridge; Eldorado; *Essexvale; Salisbury District; *Umtali; *Victoria Falls. **Bechuanaland Protectorate:** Francistown; Gaberones; Kalahari; Lobatsi; Maun; Metsimaklaba River; *Palapye; Serowe; Tsotsoroga. **Transvaal:** Barberton; Botschabelo; Crocodile and Komati Rivers; *Hectorspruit; Kurrichane; Linokana; Malelane (Malalane); Pretoria District; Shilouwane (Shilouvane). **Natal:** *Durban; Lake Sibaya; Lower Illovo River; Umfolosi Drift; Vryheid. **Cape Province:** Barkly West; Bushman Flat; Douglas; Grahamstown; Pondoland; Port St. Johns; Vaal River Diggings. **Southwest Africa:** Damaraland; Gobabis; Kuibis; Mowange; New Barmen; Okahandja; Orange River; Otjiwarongo; Outjo—north of; Paderburn Farm; Sambiu, Okawango; *Waterberg; Windhoek. **Angola:** Capangombe; Caquindo; Catumbela; Chimporo; Chitau; Cubal; Cuce River; Dundo; *Humbo; Kutato; Maconjo; Quilengues; Vila da Ponte. **Belgian Congo:** Abimva; Akenge; Albertville; Avakubi, Beni; Bugazia; Bukena; Elisabethville; Faradje; Gamangui; Kabenga; *Kabengere; Kando; Kankala River; Kanonga River;

Kapanga; Kapolowe; Kasai; Kasenyi; Kiambi; Kifuko; Kilibi; Kilwezi; Kimbili; Kunungu; Lake Tanganyika; Lofoi; Lubongola; Lubunduy River; Lukafu; Lukonzolwa; Lukuga-Niemba confluence; Lusinga; Mabwe; Makala; Makungu; Maringa; Matale—near Materne Plantation near Bukavu; Medje; Mpala; Musosa; Ngayu; Niangara; Niapu; *Njiani; Sandoa; Stanleyville; Upoto; Uvira. **Belgian Ruanda-Urundi:** Rumonge. ? **Fernando Po:** San Carlos (Bocage:1895c:more probably *s. nitidus*). **French Cameroon:** Sakdje (*fide* Monard). **Nigeria:** *Lagos (specimen bought from dealer: *nitidus* also occurs here). **Dahomey:** Agouagou; Ajuda; Cotonu. **Togo:** Kete (*nitidus* also recorded); Yendi. **Ghana:** Accra; *Adjikpo; *Christian Village; Somanya, Krobo. **Liberia:** *Gbanga; *Suacoco. **Sierra Leone:** Bonthe; Makeni; Njala. **French Guinea:** Beyla; Dixine; Dubreka; Zoubouroumai, 15 miles southeast of Macenta. **Portuguese Guinea:** Bissau (Bissao:*nitidus* also reported); Buba. **Gambia:** McCarthy Island. **French West Africa:** Bandiagara; Lobi (10° 50′N., 5°30′W.).

*Range.* Practically all Africa south of 16° N. except virgin forest areas bordering the Gulf of Guinea and certain islands therein, also a vague coastal region from southern French Congo to Angola, i.e. the range is from Gambia, east to Eritrea (not recorded from Ethiopia), south to Natal and *adjacent* Cape Province (absent from the Cape Peninsula).

### Philothamnus semivariegatus nitidus (Günther)[118]

1863c. *Ahaetulla nitida* Günther (part), Ann. Mag. Nat. Hist., (3) **11**, p. 286: No locality.

1872a. *Ahaetulla lagoensis* Günther, Ann. Mag. Nat. Hist., (4) **9**, p. 26: Lagos, Nigeria.

1875a. *Philothamnus nigrofasciatus* Buchholz & Peters, Monatsb. Akad. Wiss. Berlin, p. 199: Cameroon.

1893c. Matschie, p. 212.

1897. Sjöstedt, p. 35.

[118] Here employed in the restricted sense defined in the key. Snakes with 1 + 1 or 1 + 2 temporals occurring well within the range of *s. semivariegatus* I regard as sporadic intermediates. However, to avoid complicating or confusing the issue, I have omitted adding to *s. semivariegatus* the localities and data derived from the 30 or so individuals from the Central Lake Region assigned to *nitidus* by Laurent (1956), whose remarks should be consulted. I find no such constant frontal differences between the two forms as he suggests.

1898a. Werner, p. 209.
1882c. *Philothamnus lagoensis* Bocage, p. 6.
1894a. *Philothamnus nitidus* Boulenger, p. 100, pl. v, fig. 4.
1895. Günther, p. 528.
1896. Günther, p. 264.
1897b. Werner, p. 403.
1898a. Werner, p. 209.
1899a. Werner, pp. 137, 147, 149.
1908a. Sternfeld, pp. 408, 425.
1909a. Sternfeld, p. 15.
1909b. Sternfeld, p. 15.
1910. Müller, p. 601.
1911. Lampe, p. 193.
1917a. Phisalix, p. 334.
1919a. Boulenger, p. 282.
1929a. Werner, p. 99.
1933f. Angel, p. 110.
1936. Pitman, p. 45, pl. vi, fig. 3, pl. D, fig. 4.
1938. Pitman, pp. 39, 97, 100, 101, 179, pls. (as in 1936).
1906i. *Philothamnus semivariegatus* Boulenger (not of Smith), p. 213.
1938b. *Philothamnus semivariegatus nitidus* Mertens, p. 47.
1941a. Uthmöller, p. 42.
1951c. Loveridge (part), p. 11.
1951. Monard, p. 150.
1941. *Philothamnus semivariegatus dorsalis* Witte (not of Bocage), p. 200.

Further citations of "*nitidus*" will be found under *i. irregularis*, *s. thomensis* and *s. semivariegatus*.

*Common Name.* Cameroons Wood-Snake.

*Description.* Preoculars 1, rarely 2[119]; postoculars 2, rarely 1[120]; temporals 1 + 1, 1 + 2 or 2 + 2; upper labials 8-9, the fourth, fifth and sixth, rarely the fifth and sixth only, entering the orbit; lower labials 10-11, the first 5 or 6 in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 153-

[119] 2 preoculars in the type of *nigrofasciatus* (*fide* Buchholz & Peters).

[120] On right side only in one of the cotypes of *nitidus* (B.M. 46.1.10.28).

164 (♂♂ 153-162; ♀♀ 154-164[121]); anal divided; subcaudals 133-153 (♀♀ 133-151; ♂♂ 136-153[122]).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above, dark green. Below, chin and throat white; otherwise pale green.

*Size.* Length of ♂ (M.C.Z. 17564) 986 (610 + 376) mm., from Sakbayeme: length of ♀ (B.M. 08.5.30.17) 964 (620 + 344) mm., from Bitye.

*Remarks.* Apparently a virgin-forest form that centered in the Cameroons but is being supplanted by the typical savanna-dwelling race as the savanna encroaches on the primary forest. As a consequence occasionally both races may be recorded from one locality.

*Localities.* **French Congo:** *Benito River; *Lambarene, Ogooue River. **French Cameroon:** *Assobam; *Bitye; *Ja River District; *Kribi; Mukonje Farm, Mundame; Pungo Songo; *Sakbayeme. **British Cameroon:** Bibundi; Mowange near Mubenge; Victoria; Yaunde. **Nigeria:** *Lagos. **Togo:** Adele (Bismarckburg); Kete. **Ghana:** Accra; *Achimota.

*Range.* Virgin forests of French Congo, north through the Cameroons, west to Ghana.

### Philothamnus semivariegatus dorsalis (Bocage)

1866a. *Leptophis dorsalis* Bocage, Jorn. Sci. Lisboa, **1**, pp. 48, 69: Molembo, Loango Coast, Angola (restricted by Bocage:1882c).
1866b. Bocage, p. 69 (this is reference to full description).
1867a. Bocage, p. 226.
1876a. *Philothamnus dorsalis* Peters, p. 119.
1877c. Peters, p. 620.
1882c. Bocage, p. 9, fig. 3.
1884b. Sauvage, p. 201.
1887a. Bocage, p. 185.
1888a. Boettger, p. 58.
1894a. Boulenger, p. 101.

[121] 162 (*not* 165 as stated by Günther) in the cotype of *nitidus*.

[122] "153" in cotype of *nitidus* is now actually 151+, the tail tip being lost. These figures are all in the restricted sense of the *Range;* Belgian Congo specimens referred to *nitidus* by Schmidt (1933:78), and formerly considered as "intermediates" by me (1951c:5) on account of their temporal arrangement, are really *s. semivariegatus*.

1895a. Bocage, p. 92, pl. xiii, figs. 1a-c.
1896d. Boulenger, p. 631.
1897a. Bocage, p. 200.
1897b. Boulenger, p. 278.
1897b. Mocquard, p. 12.
1898. Boettger, p. 59.
1898. Ferreira, p. 244.
1900b. Boulenger, p. 452.
1915a. Boulenger, p. 206.
1919a. Boulenger, p. 282.
1923. Schmidt, p. 78.
1929a. Werner, p. 99.
1933m. Witte (part), p. 89.
1937b. Monard, p. 114.
1940. *Philothamnus semivariegatus dorsalis* Bogert, p. 56.
1941a. Uthmöller, p. 42 (omit).
1951e. Loveridge, pp. 5, 11.
1953. Witte, p. 198, fig. 58 (omit localities).

Further citations of "*dorsalis*" will be found under *hoplogaster, s. nitidus* and *s. semivariegatus.*

*Common Names.* Striped Wood-Snake (English); *chitelle* (S. Salvador:Bocage); *lubio* (Benguela:Bocage); *tando* (Rio Dande:Bocage).

*Description.* Preocular 1; postoculars 2, rarely 3; temporals almost always 1 + 1, very rarely 2 + 2 or 2 + 3; upper labials 9, rarely 8,[123] the fourth, fifth and sixth, rarely fourth and fifth only,[124] entering the orbit; lower labials 10-11, the first 5 in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 167-190[125] (♂♂ 167-190; ♀♀ 172-180); anal divided; subcaudals[126] 115-143 (♀♀ 115-137; ♂♂ 128-143).

*Color.* Above, snout usually yellowish brown, rest of head and body light green, bronzy green or olive, with a series of brown or black crossbars on nape and anterior part of back, usually

[123] Eight, through obvious fusion, in an Angolan ♀ (B.M.73.7.28.9).

[124] *Fide* Boulenger (1896d), checked on above mentioned ♀.

[125] Bogert (1940).

[126] This is my lowest count for a perfect tail, the specimen with 110 referred to by Bogert (1940) has a regenerated tip; a few other records under 115 have been rejected pending confirmation; 143 has been verified by a Carangigo ♀ in the British Museum.

followed by an olive brown vertebral stripe extending to tip of tail, usually many scales display a pale blue or white streak either with or without black edging. Below, labials, chin and throat yellow or white; rest of underside greenish white to yellow, usually a dusky or brownish line along the ventral keels.

Boulenger (1897b) records a specimen from Zambi, lower Congo River, with pale brown snout and white throat, but otherwise uniformly black. I have seen both these Zambi snakes (97.1.30.5-6) in the British Museum. Mocquard (1897b) mentions a Lambarene reptile in which the vertebral band was barely distinguishable. Possibly both French Congo specimens should be regarded as intermediates, or identical with *nitidus* which so often has a temporal arrangement like *dorsalis*.

*Size.* Length of ♂ (A.M.N.H. 51787) 890 (618 + 272) mm.; length of ♀ (B.M. 73.7.28.9) 857 (565 + 292) mm.

*Remarks.* It is somewhat difficult to say what should be done with the 22 snakes from Mwaya, Lake Nyasa, that I (1933h:238) previously assigned to *dorsalis* on account of their temporal arrangement being overwhelmingly of that form (cf. p. 239). In coloration they were seemingly indistinguishable from that of typical *semivariegatus* with which they are apparently surrounded. In their subcaudal counts they occupy an intermediate position, though this character may be influenced by the proportion of ♂ ♂ to ♀ ♀. In this connection the following figures are possibly of interest:

Subcaudals of 15 *dorsalis* from Lower Congo 115-136, average 122.
Subcaudals of 19 *dorsalis* from Angola 127-143, average 132.
Subcaudals of 22 snakes from Mwaya 135-156, average 144.
Subcaudals of *semivariegatus* from Africa 126-162.

It seems advisable to regard the Mwaya snakes as an isolated strain of intermediates and list them under the typical form. If only all Angolan "*semivariegatus*" could be assembled for critical study, doubtless other adjustments might be made. For example, the ♂ holotype of *bocagii*, though with *semivariegatus* coloring, tends to be intermediate in temporal arrangement, and provides the lowest subcaudal count (126) of all *semivariegatus*.

*Dentition.* Similar to that of the typical form, 20 teeth being present on the maxilla of each of two Angolan snakes examined by Bogert (1940).

*Hemipenis.* Not bifurcate; sulcus spermaticus simple; basal spines well developed, followed distally by 3 or 4 flounces merging on the middle third into reticulate calyces which grade into papillae towards the tip, which extends to the eighth caudal (Bogert).

*Localities.* **Angola:** *Benguela; Caconda; *Carangigo; Catumbela; Dombe; Dondo; Duque de Braganca; Loanda; Molembo; Pungo Andongo (Adungo); Rio Dande. **Cabinda:** Cabinda. **Belgian Congo:**[127] Banana; *Boma; Kunungu; Lower Congo River; Povo Nemlao; Sandoa; Vista; *Zambi. **French Congo:** About 7° N., 16° E. (B.M. 18.11.12.24); Lambarene (1897b); Ogoone (Ogowe:1876a).

*Range.* Angola, north along the coast to the Portuguese, Belgian and French Congo.

### Philothamnus semivariegatus girardi Bocage

1893a. *Philothamnus Girardi* Bocage, Jorn. Sci. Lisboa, (2) **3**, p. 46: "Anno-Bom," i.e. Annobon Island, Gulf of Guinea.
1893b. Bocage, p. 47.
1893d. Bocage, p. 143.
1894a. Boulenger, p. 102.
1895a. Bocage, p. 95.
1897a. Bocage, p. 200.
1903a. Bocage, p. 59.
1906i. Boulenger, p. 213.
1917. Sternfeld, p. 471.
1919a. Boulenger, p. 282.
1929a. Werner, p. 99.
1940. Bogert, p. 57.
1934c. *Philothamnus semivariegatus girardi* Mertens, pp. 27, 83, 118, 119.
1951c. Loveridge, p. 10.

[127] The alleged "*dorsalis*" from Lukafu on being examined by me proved to be a *hoplogaster;* the Kimbili and Lubongola snakes have been referred to *s. nitidus*, while, on geographical grounds, the snake from Faradje (in the extreme northeast Belgian Congo) must be considered as a *s. semivariegatus.*

The Boma ♂ (now M.C.Z. 42945), identified as *dorsalis* by de Witte, while possessing the yellow-brown snout, habitus and scale-counts (176 ventrals; 128 subcaudals: verified) lacks the subcaudal keeling and notching of the *semivariegatus* group. The number of its ventrals and subcaudals are within the range of *s. semivariegatus*, or *heterolepidotus*, but are rather higher than in *i. irregularis.*

*Common Name.* Annobon Wood-Snake.

*Description.* Preoculars 1, rarely 2; preoculars 2; temporals 1 + 1 or 1 + 2; upper labials 9-10, the fourth, fifth and sixth, or fifth, sixth and seventh, entering the orbit; lower labials 10, the first 5 in contact with the anterior sublinguals. Midbody scale-rows 13; ventrals[128] 185-197 (♀ 185); anal divided; subcaudals 143-160 (♀ 143).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above, olive green, with a longitudinal series of crossbars on nape and anterior part of back and occasionally some scales bearing a black-edged white spot. Below, greenish white or yellowish, the ventral keels black; tail bluish green.

*Size.* Total length (Bocage Mus.) 910 (595 + 315) mm.; length of a cotype ♀ (B.M. 46.1.6.3) 736 (480 + 256) mm.

*Remarks.* Known to me from a ♀ cotype (which I have examined) and the literature. This insular race is separable on its 13 midbody scale rows, a condition that is extremely rare in the continental *s. semivariegatus.*

*Locality.* Annobon Island.

*Range.* Annobon Island, Gulf of Guinea.

### Philothamnus semivariegatus thomensis Bocage

1863c. *Ahaetulla nitida* Günther (part), p. 286: "Demarara" (error) specimen only.
1879a. *Philothamnus irregularis* Bocage (not Leach), p. 87.
1885. Greef, 1884, p. 48.
1882b. *Philothamnus thomensis* Bocage, Jorn. Sci. Lisboa, **8**, p. 302: Sao Tomé Island, Gulf of Guinea.
1882c. Bocage, p. 11, fig. 4.
1886a. Bocage, p. 69.
1886. Vieira, p. 237.
1892. Bedriaga, pp. 901-903 (as *Phylothamnus*).
1893d. Bocage, p. 143.
1894a. Boulenger, p. 101.
1895a. Bocage, p. 94.
1898. Boettger, p. 59.

[128] 185 in the cotype (B.M. 46.1.6.3) which is a ♀, *not* a ♂ as stated by Boulenger (1894a:102).

1905. Bocage, p. 93.
1906i. Boulenger, p. 213.
1917. Sternfeld, p. 470.
1919a. Boulenger, p. 282.
1920a. Angel, p. 199.
1929a. Werner, p. 99.
1941. Themido, p. 6.
1934c. *Philothamnus semivariegatus thomensis* Mertens, pp. 27, 77, 91, 118, 119.
1940. Bogert, p. 57.
1951c. Loveridge, pp. 5, 10.

Further citations of "*thomensis*" will be found under *s. semivariegatus*.

*Common Names.* Sao Tome Wood-Snake (English); *soasoa* (Vieira:1886).

*Description.* Preocular 1; postoculars 2, rarely 3; temporals 1 + 1 or 1 + 2, rarely 2 + 1; upper labials 9, the fourth, fifth and sixth, or fifth and sixth only, entering the orbit; lower labials 10, the first 5 or 6 in contact with the anterior sublinguals. Midbody scale-rows 15; ventrals 200-220 (♂♂ 209-212; 206-210); anal divided; subcaudals 156-175 (♀♀ 164-168; ♂ 174).

For characters common to all species, and synopsis of scale-counts, see pp. 49-52, 55.

*Color.* Above, olive green, loreal region blackish; body uniform but the edges of the scales darker, no white spots. Below, lips and throat yellowish, otherwise pale green, the ventral keels sometimes brown.

*Size.* Total length of ♂ (B.M. 93.12.27.17) 942+ (630 + 312+) mm.; length of a ♀ (B.M. 06.3.30.76) 1242+ (825 + 417+) mm. Bogert's (1940) data disproves Bocage's idea that the tail length is diagnostic.

*Remarks.* Bedriaga's (1892) findings are ignored for the reasons stated by Bocage (1893d). The arguments advanced by Bogert (1940) for accepting Merten's action in reducing this insular form to subspecific rank are sound, and followed here.

*Breeding.* In June a ♀ held 5 eggs measuring about 37 x 8 mm. (Bogert).

*Habitat.* Occurs in coffee trees (Vieira).

*Localities.* **Sao Tome Island:**—Binda; Iogo-Iogo Islet; Obovermelho; Praia Quijo; Rodio Islet; Sandada Islet; *Vista Alegre.

*Range.* Sao Tome Island and surrounding islets, Gulf of Guinea.

## Genus PROSYMNA Gray

1849. *Prosymna* Gray, Cat. Snakes Brit. Mus., p. 80. Type by monotypy: *Calamaria meleagris* Reinhardt.

1849. *Temnorhynchus* A. Smith (not Hope), Ill. Zool. S. Africa, Rept., App., p. 17. Type by monotypy: *T. sundevallii* A. Smith.

1863. *Ligonirostra* Cope, Amer. Journ. Sci. Arts, (2) **35**, p. 457: new name for *Temnorhynchus* Smith (preoccupied in coleoptera).

1896b. *Asthenophis* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2) **17**, p. 12. Type by monotypy: *A. ruspolii* Boulenger.

1902. *Pseudoprosymna* Lindholm, in Lampe, Jahrb. Nassau Ver. Naturk. (Wiesbaden), **55**, p. 57. Type by monotypy: *P. bergeri* Lindholm = *Temnorhynchus frontalis* Peters (part).

1909c. *Stenorhabdium* Werner, Jahres. Ver. Nat. Württemberg, **65**, p. 59. Type (lost ?) by monotypy: *S. temporale* Werner.

*Definition.* Maxillary teeth 7-11, the foremost minute, the rest increasing in size posteriorly to the last 3, which are large, strongly compressed, lancet-like; palatal teeth minute, vestigial or absent; mandibular teeth few, very small, subequal. Head not distinct from neck, snout strongly depressed, projecting, with angular or sharp horizontal edge; eye relatively small, with vertically subelliptic pupil; nasal semidivided by a (sometimes interrupted or absent) horizontal suture extending from the nostril to the loreal; a preocular (usually single, occasionally absent); internasal single or paired; prefrontal usually single. Body cylindrical, short; scales smooth or keeled, with apical pits in 15-21 rows; anal entire. Tail short, terminating in a horny spine; subcaudals paired.

*Range.* Africa, in suitable terrain, south of 17° N.

*Remarks. Asthenophis* Boulenger was based on a juvenile snake whose maxillary teeth were believed to be subequal. Until this observation can be confirmed on a cleaned skull, it is best to regard it as not proven in view of the fact that the snake

differs in no other respect from *Prosymna* whose range at the time *Asthenophis* was described was supposedly remote from Somaliland.

*Pseudoprosymna* was suggested by Lindholm for a pair of snakes in which the horizontal nasal suture from the loreal failed to reach the nostril. This character is not even of specific significance since Mertens (1955a) has found it to be inconstant in *frontalis* (of which *bergeri* is considered a synonym).

*Stenorhabdium* was based by Werner on a single shrivelled snake of indefinite locality. I suggest that its condition masked its true appearance and resulted in some erroneous interpretations of what may have been a slightly aberrant *stuhlmanni*. Twenty-five years ago when I wished to see the holotype, it could not be found.

In some respects *Poecilopholis* Boulenger (1903, Ann. Mag. Nat. Hist., (7) **12**, p. 352) appears to be an offshoot of *Prosymna*. However, the type species *cameronensis* (*sic*) from Efulen, French Cameroun, lacked both supranasals and loreal, the nasal being in contact with the single preocular. Furthermore its anal shield was divided. The holotype was said to have 178 ventrals and 23 subcaudals.

In all *Prosymna* species the rostral is very large and broad, its edge often slightly upturned and more acute in old snakes, an age characteristic that has misled several herpetologists into describing as new the young or old, as the case may be. Nevertheless members of the genus fall into two groups, for in those of the *sundevallii* section the anterior edge of the rostral is sharply blade-like, rather than acutely angular. I have omitted reference to the frontal width in relation to head-width, for in several species they are subequal, the frontal being sometimes slightly more or slightly less than half the head-width; similarly it may be as long as, or slightly longer than, the parietals. In all species the single pair of enlarged sublinguals is followed by three elongate scales which are not considered as sublinguals.

Owing to the paucity of characters and the overlapping of scale-counts (more especially among the numerous races of *P. ambigua*) the construction of a satisfactory key has proved impossible. Under the circumstances those endeavoring to use it should have recourse to the geographical probabilities (cf. chart

on p. 134) and synoptic tables of statistical data — always bearing in mind that *the restricted ranges of many species* merely reflect the fact that very few individuals are known, and the ranges are *certain to be expanded* as our knowledge increases.

## *Key to the Species*[129]

1. A pair of internasals ..... 2
   A single bandlike internasal (very rarely divided) ..... 6

2. Internasals separated ..... 3
   Internasals in contact ..... 4

3. On either side a dorsolateral series of brown and black spots, also a vertebral one in which the center of each scale is yellowish or grayish white; ventrals 130-169; range: South Africa (Transvaal; Natal; Cape Province) ..... *s. sundevallii* (p. 131)
   On either side a dorsolateral, white-flecked, brown line 3 scales in width (*bivittata*), or both dorsolateral and a vertebral series of dark brown spots (*maerospila*); ventrals 159-181; range: Cape Province (Little Namaqualand) north to Southwest Africa (Okahandja) ..... *s. bivittata* (p. 136)

4. Prefrontals paired; postocular 1; range: French Sudan, French West Africa ..... *greigerti* (p. 139)
   Prefrontal single (rarely divided); postoculars 2 (rarely 1) ..... 5

5. Ventrals 114-144; subcaudals 23-38; range: British Somaliland ..... *somalica* (p. 140)
   Ventrals 155-169; subcaudals 18-20; range: Mozambique and Southern Rhodesia ..... *lineata* (p. 138)

6. Midbody scales keeled, in 15-17 rows; range: Mozambique (Inhambane) south to Natal (Kosi Bay, Zululand) ..... *jani* (p. 165)
   Midbody scales smooth, in 15-21 rows ..... 7

7. Midbody scales in 19-21 rows; ventrals 140-157; subcaudals 17-27; range: southeast Tanganyika Territory ..... *pitmani* (p. 167)
   Midbody scales in 15-17 rows ..... 8

8. Upper labials normally 5 (*rarely* 6), the second and third (*rarely* the third and fourth) entering orbit ..... 9
   Upper labials normally 6 (*rarely* 5 or 7), the third and fourth (*rarely* the second and third, or second, third and fourth) entering orbit ..10

[129] Before using, be sure to read preceding paragraph.

9. Ventrals in ♂♂ 151-160, in ♀♀ 170-184; subcaudals in ♀♀ 21-25, in ♂♂ 33-36; size larger; range: southern Sudan west through *northern* Nigeria to Senegal ... *m. laurenti* (p. 141)
   Ventrals in ♂♂ 137-150, in ♀♀ 155-166; subcaudals in ♀♀ 19-23, in ♂♂ 31-36; size smaller; range: *southern* Nigeria west through Ghana, possibly to the Ivory Coast or even Sierra Leone ... *m. meleagris* (p. 145)

10. Ventrals 160-188; subcaudals 34-51; range: western Cape Province (Little Namaqualand) north to Southwest Africa ... *frontalis* (p. 147)
    Ventrals 127-168; subcaudals 15-40; range outside of Little Namaqualand and Southwest Africa ... 11

11. Back *normally* with two longitudinal series of blackish spots; ventrals in ♂♂ ?145-155; ♀♀ ?155-163; subcaudals in ♀♀ ?16-19; ♂♂ ?25-28; range: Southwest Africa north to southwest Angola ... *angolensis* (p. 149)
    Back without longitudinal series of paired spots, normally the apex of each scale bearing a light spot ... 12

12. Subcaudals in ♀♀ 15-24; ♂♂ 25-34; range: Western Africa and Uganda ... 13
    Subcaudals in ♀♀ 19-28; ♂♂ 29-40; range: Eastern Africa and Transvaal ... 16

13. Ventrals in only known ♂ of 152; subcaudals 32; range: Belgian Ruanda-Urundi ... *a. urundiensis* (p. 156)
    Ventrals in ♂♂ 148 or less; subcaudals 25-34 ... 14

14. Ventrals in ♂♂ 139-148; ♀♀ 161-168; range: southern Sudan and Uganda west to *northern* Belgian and French Congo ... *a. bocagii* (p. 154)
    Ventrals in ♂♂ 127-140; ♀♀ 140-154 ... 15

15. Subcaudals in ♀♀ 19-24; ♂♂ 26-34; range: northwest Angola to southwest Belgian and French Congo ... *a. ambigua* (p. 151)
    Subcaudals in ♀♀ 15-17; ♂♂ 25-30; range: northeast Angola to southeast Belgian Congo ... *a. brevis* (p. 157)

16. Body with a series of scarlet blotches or crossbands; subcaudals in ♂♂ 35-40; range: Uluguru Mountains, Tanganyika Territory ... *a. ornatissima* (p. 159)
    Body without any scarlet markings; subcaudals in ♂♂ 29-37 ... 17

17. Ventrals in ♀♀ 155-158; subcaudals in ♀♀ 22-25; range: Transvaal ..... *a. transvaalensis* (p. 164)[130]
Ventrals in ♀♀ 143-155; subcaudals in ♀♀ 19-28 ..... 18

18. Subcaudals in ♂♂ 29-34; above gray or plumbeous, uniform or with a dorsolateral series of white flecks; range: Kenya Colony south to Zululand, Natal ..... *a. stuhlmanni* (p. 160)
Subcaudals in ♂♂ 32-37; above dark reddish to purplish brown; usually a light spot on the apex of each scale; range: Somalia ..... *a. ruspolii* (p. 158)

That a burrowing genus like *Prosymna* has been reported from "Zanzibar" alone of the ten major islands off the coasts of tropical Africa, suggests that the specimen in question came from the opposite littoral, to which the name Zanzibar was formerly applied rather loosely. More surprising is the fact that no member of the genus has been recorded from Eritrea, Ethiopia, French Somaliland, Bechuanaland, Cabinda, Rio Muni or Liberia.

### Prosymna sundevallii sundevallii (Smith)

1849. *Temnorhynchus Sundevallii* (*sic*) A. Smith, Ill. Zool. S. Africa, Rept., app. p. 17; Kaffirland, eastward of Cape Colony, i.e. Cape Province, Union of South Africa.
1887h. Boulenger, p. 175.
1858e. *Rhinostoma cupreum* Günther, Cat. Colubrine Snakes Brit. Mus., p. 9: Africa.
1894a. *Prosymna sundevallii* Boulenger, p. 247.
1895. Jeude, p. 229.
1896c. Bocage, p. 119.
1898. Sclater p. 99.
1898. Werner, p. 144.
1907e. Roux, p. 735.
1908. Gough, p. 24.
1910b. Boulenger (part), p. 508 (omit L. Namaqualand?).
1910. Lönnberg, p. 5
1912. FitzSimons, F. W., p. 88.
1913. Hewitt & Power, p. 162.
1916g. Chabanaud, p. 438.

[130] *P. a. transvaalensis* Hewitt appears doubtfully distinct, possibly nearer to *a. ambigua* than to *a. stuhlmanni;* geographically it occupies an intermediate position.

## STATISTICAL DATA FOR THE SPECIES OF *PROSYMNA*

| Species or race | Scales | Internasal | Pre-ocular | Post-oculars | Temporals |
|---|---|---|---|---|---|
| *s. sundevallii* | 15 | 2 separate | 1 | 2-3 | 1+2 1+3 2+2 2+3 |
| *s. bivittata* | 15 | 2 separate | 1 | 2 | 1+1 1+2 2+3 |
| *lineata* | 15 | 2 contact | 1 | 2 | 1+2 2+2 |
| *greigerti* | 15 | 2 contact | 1 | 1 | 1+2 |
| *somalica* | 15 | 2 contact | 1-2 | 1 | 1+2 |
| *m. laurenti* | 15 | 1 rarely 2 | 1 | 1-2 | 1+1 1+2 1+3 2+2 |
| *m. meleagris* | 15 | 1 | 1 | 1 | 1+1 1+2 1+3 |
| *frontalis* | 15 | 1 | 1 | 1-2 | 1+2 |
| *angolensis* | 15 | 1 | 1 | 1-2 | 1+2 |
| *a. ambigua* | 15-17 | 1 | 1 | 1-2 | 1+1 1+2 2+2 |
| *a. brevis* | 15 | 1 | 1 | 1-2 | 1+2 |
| *a. bocagii* | 15 | 1 | 1 | 1-2-3 | 1+1 1+2 2+2 |
| *a. urundiensis* | 15 | 1 | 1 | 2 | 1+2 |
| *a. ruspolii* | 15 | 1 | 1 | 1 | 1+2 |
| *a. ornatissima* | 15 | 1 | 1 | 0-1-2 | 1+2 |
| *a. stuhlmanni* | 15 | 1 | 0-1 | 0-1-2 | 1+1 1+2 1+3 2+2 |
| *a. transvaalensis* | 15 | 1 | 1-2 | 0-1-2 | 1+1 1+2 1+3 2+3[131] |
| *jani* (keeled) | 15-17 | 1 | 1 | 2-3 | 1+2 |
| *pitmani* | 19-21 | 1 | 1-2 | 2 | 1+2 2+2 |

[131] Not 1 + 3 but 2 + 3 in paratype, *fide* FitzSimons (10.v.57).

| Species or race | ♂♂ ventrals | ♀♀ ventrals | ♀♀ subcaudals | ♂♂ subcaudals | Maximum length[132] ♂♂ | Maximum length[132] ♀♀ |
|---|---|---|---|---|---|---|
| *s. sundevallii* | ?130-155 | ?155-169 | ?19-27 | 28-38 | 230+35 | 280+30 |
| *s. bivittata* | ?159-167 | ?178-181 | ?22-23 | ?25-29 | 221+24 | 315+27+ |
| *lineata* | | 155-169 | 18-20 | | | 259+23 |
| *greigerti* | | 168 | 18 | | | 159+13 |
| *somalica* | 114-126 | 132-144 | 23-29 | 30-38 | 154+39 | 104+15 |
| *m. laurenti* | 151-160 | 170-184 | 21-25 | 33-36 | 238+42 | 332+28 |
| *m. meleagris* | 137-150 | 155-166 | 19-23 | 31-36 | 220+37 | 255+24 |
| *frontalis* | 160-169 | 180-188 | 34-38 | 48-51 | 244+56 | 312+43 |
| *angolensis* | ?145-155 | ?155-163 | ?16-19 | ?25-28 | | 331+29 |
| *a. ambigua* | 129-140 | 145-154 | 19-24 | 26-34 | 237+46 | 313+32 |
| *a. brevis* | 127-136 | 140-146 | 15-17 | 25-30 | 267+48 | 325+26 |
| *a. bocagii* | 139-148 | 161-168 | 17-21 | 27-32 | 250+48 | 366+32 |
| *a. urundiensis* | 152 | | | 32 | 199+36 | |
| *a. ruspolii* | 130-136 | 143-154 | 23 | 32-37 | 165+33 | 262+33 |
| *a. ornatissima* | 127-132 | 150 | 27 | 35-40 | 242+55 | 252+34 |
| *a. stuhlmanni* | 129-144 | 144-155 | 19-28 | 29-34 | 200+38 | 293+30 |
| *a. transvaalensis* | | 155-158 | 24-26 | | | 255+25 |
| *jani* (keeled) | ?113-119 | | | ?30-37 | 188+36 | |
| *pitmani* | 140-151 | 155-157 | 17-20 | 25-27 | 275+34 | 285+23 |

[132] Maximum lengths are given in millimetres, first of the head and body, then that of the tail; added together they give the total length. Where a question mark (?) precedes figures it denotes that the sex is assumed, at least in part owing to the sex having been omitted by the describer. Sexual dimorphism being so strongly marked in this genus, the assumption has usually a sound basis.

| Recorded distribution of *Prosymna* around the African continent | sundevallii sundevallii | sundevallii bivittata | lineata | greigerti | somalica | meleagris laurenti | meleagris meleagris | frontalis | angolensis | ambigua ambigua | ambigua brevis | ambigua bocagii+urundiensis | ambigua ruspolli | ambigua ornatissima | ambigua stuhlmanni | ambigua transvaalensis | jani | pitmani |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sudan | | | | | | * | | | | | | * | | | | | | |
| British Somaliland | | | | | * | | | | | | | | | | | | | |
| Somalia | | | | | | | | | | | | | * | | | | | |
| Uganda Protectorate | | | | | | | | | | | | * | | | | | | |
| Kenya Colony | | | | | | | | | | | | | | | * | | | |
| Tanganyika Territory | | | | | | | | | | | | | | * | * | | | * |
| Zanzibar Island | | | | | | | | | | | | | | | * | | | |
| Mozambique | | | * | | | | | | | | | | | | * | | * | |
| Nyasaland | | | | | | | | | | | | | | | * | | | |
| Northern Rhodesia | | | | | | | | | | | | | | | * | | | |
| Southern Rhodesia | | * | * | | | | | | | | | | | | * | | | |
| South Africa: | | | | | | | | | | | | | | | | | | |
| (Transvaal) | * | | | | | | | | | | | | | | | * | | |
| (Natal & Zululand) | * | | | | | | | | | | | | | | * | | * | |
| (Cape Province) | * | * | | | | | | * | | | | | | | | | | |
| Southwest Africa | | * | | | | | | * | * | | | | | | | | | |
| Angola | | | | | | | | | * | * | * | | | | | | | |
| Belgian Congo | | | | | | * | | | | * | * | * | | | | | | |
| Belgian Ruanda-Urundi | | | | | | | | | | | | * | | | | | | |
| French Congo | | | | | | * | | | | * | | * | | | | | | |
| British Cameroon | | | | | | * | | | | | | | | | | | | |
| Nigeria | | | | | | * | * | | | | | | | | | | | |
| Dahomey | | | | | | | * | | | | | | | | | | | |
| Togoland | | | | | | | * | | | | | | | | | | | |
| Ghana (Gold Coast) | | | | | | | * | | | | | | | | | | | |
| Ivory Coast | | | | | | | * | | | | | | | | | | | |
| Sierra Leone | | | | | | * | * | | | | | | | | | | | |
| Portuguese Guinea | | | | | | * | | | | | | | | | | | | |
| Gambia | | | | | | * | | | | | | | | | | | | |
| Senegal | | | | | | * | | | | | | | | | | | | |
| French West Africa | | | | * | | * | | | | | | | | | | | | |

1929. Flower, p. 218.
1929a. Werner, p. 141.
1937a. FitzSimons, V. F., p. 262.
1946a. FitzSimons, V. F., p. 355.
1950. Rose, p. 320, fig. 10.
1955. Rose, pp. 96, 178, fig. 10 (reprinted).

Further citations of "*sundevallii*" will be found under *s. bivittata* and *meleagris*.

*Common Name.* South African Shovel-snout (A.L.); Coppery Snake (F. W. FitzSimons).

*Description.* Rostral with sharp horizontal edge; internasals separated, occasionally in contact by their inner angles;[133] prefrontal single, rarely divided[133]; frontal large; loreal as long as high or slightly higher; preocular 1; postoculars 2-3; temporals rarely 1 +2 or 1+ 3, usually 2 +2 or 2+ 3; upper labials 6-8, the third and fourth, rarely fourth and fifth entering the orbit; lower labials 7-8, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 130-169[134] (assumed ♂ ♂ 130-155; assumed ♀ ♀ 155-169); anal entire; subcaudals 19-38 (assumed ♀ ♀ 19-27; definite ♂ ♂ 28-38).

*Color.* Above, rostral and crown yellowish white, or head yellowish with a more or less distinct dark brown interocular band and a dark brown crescentic blotch bordering the parietals posteriorly; body pale gray to reddish brown, sometimes each scale edged with darker, the center of each vertebral scale yellow or grayish white, on either side a dorsolateral series of small brown or black spots extend along the back. Below, white or yellowish, uniform or with dusky blotches and a reddish median line along the tail.

*Size.* Length of ♂ (M.C.Z. 21243) 265 (230 + 35) mm., from Sunnyside; length of ♀ (M.C.Z. 21244) 310 (280 + 30) mm., from Meintjeskop, both localities being near Pretoria.

*Remarks.* Sir A. Smith, whose scale counts were often erroneous, states that the type had 169 ventrals, a figure I should be

[133] *fide* Boulenger (1894a), possibly by inclusion of mistakes in the literature.

[134] Omitted are the figures of a juvenile recorded by Boulenger (1894a) as having 125 ventrals and 27 subcaudals.

inclined to question as it is 5 more than found on any subsequently recorded specimen. However, FitzSimons (1937a) reports that a specimen in poor preservation, but corresponding to the type in lepidosis and measurements, is among the Smith collection in the Royal Scottish Museum, Edinburgh.

*Localities.* **Transvaal:** Assegaibos; Brakkloof; Crocodile-Komati (Comati) River Junction; Harts River; Krabbefontein; *Meintjeskop; *Sunnyside. **Natal:** Durban. **Cape Province:** Burghersdorp; Clanwilliam; Fort Richmond; Graaf Reinet; Hanover; Kaffirland; Orange River; Tulbagh.

*Range.* Union of South Africa, from the Transvaal southwest to Little Namaqualand where it meets with *sundevallii bivittata* (including *macrospila*).

### Prosymna sundevallii bivittata Werner

1867b. *Temnorhynchus frontalis* Peters (part:not Peters 1867b), p. 236, pl. —, figs. 2-2d: Southwest Africa.
1902a. *Prosymna sundevallii* Werner (not Smith), p. 339.
1910b. Sternfeld, p. 20, fig. 20.
1915c. Werner, p. 360.
1929a. Werner, p. 141.
1903. *Prosymna sundevallii* var. *bivittata* Werner, Abhand. König. Bayer. Akad. Wiss., **22**, p. 381: Africa south of the Orange River, i.e. Little Namaqualand.
1910a. Werner, p. 327.
1915c. Werner, p. 360.
1916g. Chabanaud, p. 439.
1955a. Mertens, p. 95.
1910a. *Prosymna sundevallii* var. *macrospila* Werner, Denkschr. Med.-Nat. Ges. Jena, **16**, p. 357: Steinkopf, Little Namaqualand.

*Common Name.* Two-striped Shovel-snout (A.L.).

*Description.* As in the typical form, with prefrontal single, rarely divided[135]; temporals 1 + 2, 2 + 2, or 2 + 3[136]; ventrals 159-181; subcaudals 22-29. This form agrees with *s. sundevallii* in having widely separated internasals, but approaches *frontalis* in its high ventral count.

[135] Divided in the adult mentioned by Werner (1910a); confirmed by Mertens (1955).

[136] 2 + 3 in the holotype of *macrospila*.

*Color of var. bivittata.* Above, an interocular brown band and a transverse, hourglass-shaped, dark brown blotch on the nape from which there extends backwards a pair of parallel, white-flecked, brown lines three scales in width; on either flank the three outermost rows of scales are white. Below, white, uniform.

*Color of var. macrospila.* Above, head yellowish, a brown band across the nasals and prefrontal; also brown are the anterior borders of the frontal and supraoculars in addition to a spot under either eye; body yellowish, a vertebral series of angularly shaped, or obliquely elliptical, dark brown spots, a dorsolateral series of similar spots along the back. Below, whitish, uniform.

Essexvale ♀ with 181 ventrals. Above, dark purplish brown; rostral lighter; upper labials cream colored; frontal with a dull orange (turned brown in alcohol) blotch; parietals with smaller blotches; back with a vertebral stripe three scales in width but interrupted by numerous X or V-shaped purplish brown markings; lower flanks have the outermost 1½ or 2 scale rows cream colored. Below, cream colored, uniform. Based on notes made from this snake in life by D. G. Broadley.

*Size.* Length of ♂ (S.M.F. 32542) 245 (221 + 24) mm., from "Deutsch-Südwestafrika"; largest ♀ (S.R.M. 635) 342+ (315 + 27+) mm., from Essexvale; length of *bivittata* type (presumably an adult ♀) 296 (275 + 21) mm.; length of *macrospila* type (presumably a juvenile ♀) 156 (141 + 15) mm.

*Remarks.* As suggested by its size, *macrospila* may represent the juvenile coloring for Werner (1910a) clearly states that he regards it as but another color variety, saying he has both varieties from Steinkopf. In the same paper he mentions three *bivittata*, the most northerly example coming from Okahandja. Mertens (1955), who rightly recognizes the race, has also seen three specimens of it. The only one I have handled is from Essexvale, the first record from Southern Rhodesia, where it was collected by D. G. Broadley.

*Localities.* **Southern Rhodesia:** *Essexvale. **Little Namaqualand:** South of Orange River (*bivittata* type); Steinkopf (*macrospila* type). **Southwest Africa:** Okahandja; Otjimbingue; Windhoek.

*Range.* Southern Rhodesia, west to Little Namaqualand, north to Damaraland, Southwest Africa.

### Prosymna lineata (Peters)

1871a. *Temnorhynchus lineatus* Peters, Monatsb. Akad. Wiss. Berlin, p. 568: Matlale, Gazaland, Mozambique.
1882a. *Prosymna frontalis* Bocage (part: not Peters), p. 288.
1895a. Bocage, p. 99.
1896a. *Prosymna Sundevallii* (*sic*) Bocage (not Smith), p. 92
1953e. *Prosymna lineata* Loveridge, p. 264.

*Common Name.* Mozambique Shovel-snout (A.L.).

*Description.* Rostral with sharp horizontal edge; separated by a pair of internasals (that are broadly in contact) from the single bandlike prefrontal; frontal large; loreal as long as high; preocular 1; postoculars 2; temporals 1 + 2, 2 + 2 or 2 +3; upper labials 5-6, the third and fourth entering the orbit; lower labials 8, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 155-169 (♀ ♀ 155-169); anal entire; subcaudals 18-20 (♀ ♀ 18-20).

*Color.* Above, head brown with black markings on the prefrontal; body dark violet brown, some scales edged with black and others flecked with white and coalescing to form a ladderlike pattern on the dorsum. Below, yellowish white, uniform.

Juvenile ♀ from Plumtree. Above, pale gray; internasals with a black crossbar; prefrontal with a spectacle-like crossbar as its extremities encircle the orbits; frontal with a black spot posteriorly; a black, T-shaped, nuchal marking; dorsum and tail with a series of irregular, light-edged, dark blotches that do not coalesce with the ill-defined line that flanks them. Below, white, uniform.

*Size.* Length of holotype ♀ (Berlin Mus.) 282 (259 + 23) mm. In the figures furnished by Peters there was a major (probably printer's) error; I am indebted to Dr. Heinz Wermuth for those given above. That this was a very large *Prosymna* was obvious from the head length — 9 (not 11) mm., and body diameter of 9 mm.; length of juv. ♀ (S. R. Mus.) 130 (120 + 10) mm., from Plumtree.

*Remarks.* Peters rightly compared his new species to *frontalis*, with which Bocage erroneously synonymized it. Boulenger overlooked *lineata* altogether. I obtained the third known example (M.C.Z. 51144) under the peculiar circumstances mentioned

below. A fourth was obtained by A. E. Strover, a scholar of Plumtree School, in March, 1954. Still more recently I have seen another ♀ taken at Selukwe by A. H. R. Stevenson.

*Enemies.* The tailless, much-chewed remains of a large *lineata* were present in the stomach of a topotypic Mozambique Genet (*Genetta tigrina mossambica*) that was basking, shortly after sun-up, high in a big baobab where I shot it.

*Localities.* **Mozambique:** Angoche; *Kasumbadedza near Tete; Matlale (type). **Southern Rhodesia:** *Plumtree; *Selukwe.

*Range.* Mozambique, west through Southern Rhodesia.

### Prosymna greigerti Mocquard

1906c. *Prosymna Greigerti* Mocquard, Bull. Mus. Hist. Nat. (Paris), **12**, p. 466: Lobi region, French Sudan, i.e. French West Africa.
1916g. Chabanaud, p. 438.
1919a. Boulenger, p. 285.
1929a. Werner, p. 142.
1933f. Angel, p. 125, figs. 47-47a.
1950b. Villiers, p. 87, fig. 112.

*Description.* Rostral with angular horizontal edge, separated by a pair of internasals from the paired prefrontals; frontal large; loreal longer than high; preocular 1; postocular 1; temporals 1 + 2; upper labials 5, the second and third entering the orbit; lower labials ?, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 168; anal entire; subcaudals 18.

*Color.* Above, chestnut brown, duller on the neck; on temporal region, sides of neck, and rest of body, each scale has a white central spot. Below, lips and throat dusky, otherwise whitish, uniform.

*Size.* Length of holotype, presumably a ♀ (Paris Mus.), 173 (159.5 + 13.5) mm.

*Remarks.* Since Lt. Greigert collected the type almost fifty years ago, no second example has been taken. The type locality is near the northwest frontier of the Gold Coast and the northeast Ivory Coast. In view of Chabanaud's recording of an aberrant

*melcagris* with paired internasals at Dagana, Senegal, the possibility that *greigerti* (whose paired internasals and paired prefrontals chiefly separate it from *melcagris laurenti*) is also an aberrant, should be borne in mind.

### Prosymna somalica Parker

1930b. *Prosymna somalica* Parker, Ann. Mag. Nat. Hist., (10) **6**, p. 605: Haud, 8° N., 47°22′ E., at 2,000 feet, British Somaliland.
1932b. Parker, p. 364.
1949a. Parker, p. 64.

*Common Name.* Northern Somaliland Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge; separated by a pair of internasals from the single, very rarely divided (B.M.1949.2.1.91 only) prefrontal; frontal large; loreal longer than high; preocular 1, rarely 2 (B.M.1949.2.1.94); postocular 1; temporals 1 + 2; upper labials 6, the third and fourth entering the orbit; lower labials 8, the first three in contact with the sublinguals. Midbody scale-rows 15, smooth; ventrals 114-144 (♂♂ 114-126; ♀♀ 132-144); anal entire; subcaudals 23-38 (♀♀ 23-29; ♂♂ 30-38).

*Color.* Above, dark purplish brown, the free edge of each scale margined with lighter. Below, white, usually uniform, the throat sometimes invaded by the darker dorsal coloring.

*Size.* Length of holotype ♂ (B.M.1930.5.9.12) 193 (154 + 39) mm.; length of ♀ (Parker: 1932b) 119 (104 + 15) mm.

*Remarks.* Only a single pair of sublinguals are well developed; the three following scales do not differ appreciably from the corresponding scales in other species of *Prosymna*, though in the holotype of *somalica* they were actually longer than the anterior pair. While assuming this most northerly representative of the genus is ancestral to its neighbor *a. ruspolii* to the south, with which it has much in common, I agree with Parker as to its specific distinctness.

*Dentition.* Parker (1949a) invites attention to the less specialized development of the posterior maxillary teeth which, in a 250 mm. *somalica*, measure only 1.0 mm. as against 1.6 mm. in an *ambigua stuhlmanni* of similar size.

*Habitat.* In addition to the type, taken at 2000 feet, Colonel R. H. R. Taylor secured a dozen other examples at altitudes ranging from 3500 to 4500 feet, in stone-strewn sandy terrain whose scant vegetation consisted largely of acacia-euphorbia bush interspersed with patches of grass.

*Localities.* **British Somaliland:** Bohodle; Borama District; Burao; Haud (many positions being designated by latitude and longitude).

*Range.* British Somaliland.

### Prosymna meleagris laurenti subsp. nov.

1843. *Calamaria meleagris* Reinhardt (part: ♀ only; omit ♂), K. Danske Vidensk. Selsk. Afhandl., **10**, p. 238, pl. i, figs. 4-6: "Guinea," as old museum specimen, possibly near Gambia?
1849. *Prosymna meleagris* Gray (part[137]), p. 80.
1862. Jan, p. 55 (? Sierra Leone).
1894a. Boulenger, p. 249.
1908a. Sternfeld, pp. 409, 425.
1909b. Sternfeld, p. 17.
1915d. Boulenger, p. 649.
1916g. Chabanaud, p. 440 (French Congo and Sudan only).
1919a. Boulenger, p. 285.
1922. Aylmer, p. 15 (but possibly not this race).
1922a. Angel, p. 39.
1929a. Werner, p. 142, fig. 40.
1933f. Angel, p. 126, fig. 48.
1937. Andersson, p. 8.
1938. Angel & Lhote, p. 366.
1950a. Villiers, p. 70.
1950b. Villiers, p. 87, fig. 113.
1951. Monard, p. 151.
1954b. Laurent, p. 57.
1956c. Loveridge, 1955, p. 45.
1884a. *Temnorhynchus sundevallii* Rochebrune (not Smith), p. 149.
1884a. *Temnorhynchus meleagris* Rochebrune (not Reinhardt), p. 150.
1884a. *Temnorhynchus frontalis* Rochebrune (not Peters), p. 150.
1884a. *Temnorhynchus ambiguus* Rochebrune (not Bocage), p. 151 (all four of these Rochebrune references are ignored).
1918b. *Prosymna meleagris collaris* Chabanaud (not Sternfeld), p. 164.
1933m. *Prosymna ambigua* Witte (part: not Bocage), p. 91 (Kunungu).

[137] Inevitably many of the following citations are in part only, though preponderately the new form. See also citations under *meleagris*.

*Common Name.* Sudanese Shovel-snout (A.L.).

*Holotype.* Museum of Comparative Zoology No. 53383, an adult ♂ from Mongalla, Equatoria Province, Sudan, collected by John Owen, Esq., between May and August, 1950.

*Paratypes.* Twenty ♂ ♂ and ten ♀ ♀ from Equatoria, viz. Museum of Comparative Zoology Nos. 53377-53392 (less 53383), from five localities (Lokwi; Magwe; Mongalla; Okaru; Torit); also Chicago Natural History Museum Nos. 48070-2, 58402-4, 58406-8, 58443, 62233-6, 62238-9, from three localities (Katire; Molongori; Torit), all collected by John Owen.

*Diagnosis. Calamaria meleagris* was described by Reinhardt on the basis of two specimens (a third, subsequently seen, receives passing mention in a postscript), obviously a ♂ and ♀, though this is not stated. Both were from "Guinea," a name that in 1843 was applied to any of the countries bordering the Gulf of Guinea from Portuguese Guinea to the French Congo. Fortunately Reinhardt states that his two snakes had different origins. One formed part of a collection sent to Copenhagen Museum in 1836 by Herr Chenon, assistant to the "government establishment on the coast." Presumably he refers to Christiansborg, one-time seat of Danish administration on the coast of Ghana near Accra, for the various species of snakes donated by Chenon are still common in Ghana. The smaller ♂, the main basis of Reinhardt's description, agrees in every way with Ghana *m. meleagris* as here defined.

Reinhardt's second snake (presumably the larger ♀) was said to have come from the collection of the "old natural history society." As its scale-counts fall within the range of the Sudanese race it may have come from the general region of Gambia, alternatively, though less likely at that early date, from the interior of Nigeria or Cameroon. Owing to the description of *meleagris* being based on both races, the separation of the forms has been obscured until now. Indeed it was not until I was able to assemble adequate series from Ghana (22 specimens) and the Sudan (31 examples) that the respective ranges in ventral and subcaudal counts could be demonstrated.

| Race | No. & Sex | Ventrals | Caudals | Largest example |
|---|---|---|---|---|
| *m. meleagris* | 15 Ghana ♂♂ have | 137-150; | 31-36; | 257 (220 + 37) mm. |
| *m. laurenti* | 21 Sudan ♂♂ have | 151-160; | 33-36; | 280 (238 + 42) mm. |
| *m. meleagris* | 8 Ghana ♀♀ have | 155-166; | 19-23; | 270 (255 + 24) mm. |
| *m. laurenti* | 10 Sudan ♀♀ have | 170-184; | 21-25; | 360 (332 + 28) mm. |

*Description of holotype.* ♂. Midbody scale-rows 15; ventrals 158; subcaudals 36; preocular 1; postocular 1; temporals 1 + 2.

*Description.* Rostral with angular horizontal edge; separated by the single, rarely divided,[138] bandlike internasal from the single prefrontal; frontal large; loreal longer than high, rarely divided[138]; preocular 1; postocular 1[139]; temporals 1 + 1 or 1 + 2, rarely 1 + 3 or 2 + 2[140]; upper labials 5, rarely 6, the second and third, rarely the third and fourth,[141] entering the orbit; lower labials 7-8, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 151-184[142] (♂♂ 151-160; ♀♀ 170-184); anal entire; subcaudals 21-36[143] (♀♀ 21-25; ♂♂ 33-36).

*Color.* Above, head black or brown, except for rostral and labials which may be white; body pale brown (juvenile) to black (adult), each scale with a whitish terminal spot. Below, white to yellowish white, the dorsal pigmentation usually impinging on either side of the ventrals in the region of the neck; occasionally chin and throat brown,[144] otherwise uniform.

Chabanaud (1918b) refers to *collaris* a Dagana snake that he describes as being: Above, a rather deep rosy brown; head uniform except for a pair of large white spots on the parietals posteriorly; on either side of the neck the white underside extends

[138] Divided, yet in contact by their anterior angles while separated posteriorly by an azygous, triangular shield whose base rests on the center of the bandlike prefrontal, only in a Dagana snake recorded by Chabanaud (1918b).

[139] Two in a Kunungu ♀ (R.G.M.C. 5676) *fide* Laurent (1945b).

[140] 2 + 2 in only one (C.N.H.M. 58403) of 22 Torit snakes.

[141] Six, the third and fourth entering the orbit only on side of a Mongalla ♀ (M.C.Z. 53384).

[142] 151 in a Torit ♂ (M.C.Z. 53388); 184 in a Torit ♀ (C.N.H.M. 48070).

[143] 19 in a McCarthy Id. snake (*fide* Andersson 1937); 21 in several Torit ♀♀; 25 in a Lokwi ♀ (M.C.Z. 53378), and, but not checked, 26 in a Poli specimen (Vienna Mus.).

[144] Brown only in a Torit ♂ (C.N.H.M. 62234).

upwards to form a collar that almost meets in a point on the median line of the nape; on the rest of the back each scale bears a whitish terminal spot. Below, throat brown in advance of the collar, otherwise under surface white, uniform.

Assuming this *Prosymna* from Dagana is referable to the Sudanese form — as would appear from the ventral counts of two Gambia snakes furnished by Andersson — *collaris* appears to be only a color phase occurring erratically within the ranges of either race of *meleagris*. There remains a possibility that snakes from the extreme west may represent yet another race of *meleagris*, something that can be demonstrated only by assembling all the known material from the region.

From Poli, in northwest Cameroon, we have a gravid ♀ with heavy black collar which looks rather different from the extensive Sudanese series. In this it would seem to resemble the Yola (Jola) snake mentioned by Sternfeld (1908a) from northeast Nigeria, both localities being near Garoua. Ventral counts of three other Poli snakes in Vienna Museum (but unsexed) indicate they are referable to the Sudanese race, though slightly intermediate as might be expected.

*Size.* Length of type, the largest ♂ (M.C.Z. 53383) 280 (238 + 42) mm., from Mongalla; largest ♀ (C.N.H.M. 48070) 360 (332 + 28) mm., from Torit.

*Dentition.* Maxillary teeth 6, the anterior 4 minute, the last 2 large; an arrangement strikingly different from that of *angolensis fide* Laurent (1954b).

*Sexual dimorphism.* In addition to the marked difference in the number of ventrals and subcaudals (as may be seen by reference to the *Description*) the tail is distinctly longer in ♂ ♂, as may be seen from the following figures:

In 13 Sudan ♂ ♂, tail is included in H. & B. length 5.6 to 6.3 times; in 9 Sudan ♀ ♀, tail is included in H. & B. length 10.0 to 11.9 times.

*Habitat.* Most of the Sudan series were hoed up during cultivation, but two of them were found beneath rubbish in Owen's garden.

*Localities.* **Sudan:** *Katire; *Lokwi; *Magwe; *Molongori; *Okaru; *Torit. **Belgian Congo:** Kunungu. **French Congo:** (as *meleagris; fide* Chabanaud). **British Cameroon:** *Poli near

Garoua. **Nigeria:** *Yola (Jola). **Sierra Leone:** (*fide* Jan:1862). **Portuguese Guinea:** Mansoa. **Gambia:** McCarthy Island. **Senegal:** Dagana. **French West Africa:** Dano near Diebougou, Upper Volta; French Sudan; Kati, 12 km. north of Bamakko, Beldogou; San; Thies.

*Range.* Southern Sudan westward through northern Belgian Congo, northern Cameroon, northern Nigeria, to Senegal, i.e. from about 3° S. of the equator in Central Africa to almost 20° N. on the west coast.

### Prosymna meleagris meleagris (Reinhardt)

1843. *Calamaria meleagris* Reinhardt (part: ♂ only; omit ♀), K. Danske Vidensk. Selsk. Afhandl., **10**, p. 238, pl. i, figs. 4-6: "Guinea," as Chenon coll., probably Ghana.
1849. *Prosymna meleagris* Gray (part[145]), p. 80.
1862. Jan, p. 55.
1885. Müller, p. 678.
1894a. Boulenger, p. 249.
1896d. Boulenger, p. 641.
1901b. Werner, p. 638.
1903. Gough, p. 466.
1910. Lönnberg, p. 6.
1915d. Boulenger, p. 649.
1916f. Chabanaud, p. 372 (Dahomey and Ivory Coast only).
1916g. Chabanaud, p. 440.
1917b. Chabanaud, p. 11.
1917a. Phisalix, p. 333.
1919a. Boulenger, p. 285.
1922. Aylmer, p. 15 (but possibly not this race).
1929. Flower, p. 218.
1929a. Werner, p. 142, fig. 40.
1933f. Angel, p. 216, fig. 48.
1945. Leeson, p. 1.
1950. Leeson, pp. ix, 64-66, 134, fig. 30.
1875a. *Temnorhynchus meleagris* Peters, p. 198.
1908b. *Prosymna meleagris* var. *collaris* Sternfeld, Mitt. Zool. Mus. Berlin, **4**, pp. 216, 231: Misahöhe, Togo, Ghana (restricted).
1909a. Sternfeld, p. 16, fig. 24.
1916g. Chabanaud, p. 440.

[145] Inevitably most of the following citations are also in part only; for others, see citations under the new subspecies.

Further citations of "*meleagris,*" including *meleagris concolor* Lönnberg, will be found under *a. ambigua.*

*Common Names.* Ghana Shovel-snout (A.L.); Reinhardt's Ground-Snake (Flower).

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single prefrontal; frontal large; loreal longer than high; preocular 1; postocular 1; temporals 1 + 2; upper labials 5, rarely 6, the second and third, rarely the third and fourth[146] entering the orbit; lower labials 7-8, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 137-166[147] (♂♂ 137-150; ♀♀ 155-166); anal entire; subcaudals 19-36[148] (♀♀ 19-23; ♂♂ 31-36).

*Color.* Typical. Above, head black or brown, except for rostral and labials which may be white; body pale brown (juvenile) to black (adult), each scale with a whitish terminal spot. Below, white to yellowish white, the dorsal pigmentation usually impinging on either side of the ventrals in the region of the neck: occasionally chin and throat brown, otherwise uniform.

Var. *collaris.* Said by Sternfeld to exhibit two longitudinal, posteriorly converging, white marks in the parietal region, while the dark portion of the nape is bordered posteriorly by a white nuchal collar. This coloration, says Sternfeld, is exhibited by several Togo snakes of various ages whose lepidosis in no way differs from those of other specimens. This kind of coloration is present in our smallest *m. meleagris* ♀ (M.C.Z. 55231) from Pong-Tamale, Northern Territory, Ghana, which measures 124 (114 + 10) mm. However, the first pair of white blotches are situated on the temporal region and barely impinge on the parietals; two scale-rows behind the parietals there is a larger pair of white spots on the nape, closely followed by a broad black bar narrowly edged posteriorly with white. There is no trace of such markings in a juvenile ♂ (M.C.Z. 53697) from near Achimota, Ghana, yet only 1 mm. longer in body length

[146] Six, the third and fourth entering orbit on one side only of a Niger snake (Gough :1903).

[147] 137 in ♂♂ from Somanya (M.C.Z. 55229) and Lagos (C.N.H.M. 41119); 166 in ♀♀ from Achimota (M.C.Z. 53693 and C.N.H.M. —).

[148] 19 in an Achimota ♀ (C.N.H.M. —); 36 in ♂♂ from Achimota and Lagos (C.N.H.M. 41119).

than the ♀. It is doubtful if any significance attaches to this variant as it has been recorded from as far away as Dagana, Senegal (see *Remarks* under the Sudanese subspecies).

*Size.* Largest ♂ (M.C.Z. 53698) 257 (220 + 37) mm., from Achimota; largest ♀ (M.C.Z. 55224) 279 (255 + 24) mm., from Somanya.

*Anatomy.* No parotids present (Phisalix).

*Sexual dimorphism.* In addition to the marked difference in the number of ventrals and subcaudals, as may be seen by reference to the *Description*, the tail is distinctly longer in ♂ ♂. Thus:

In 12 Ghana ♂ ♂, tail is included in H. & B. length 5.4 to 6.6 times.

In 8 Ghana ♀ ♀, tail is included in H. & B. length 10.3 to 11.6 times.

*Habitat.* A Lagos and several of the Achimota snakes were found in roadside gutters intended for carrying off rain water. Most Somanya snakes were dug up by labourers.

*Localities.* **Nigeria:** Lagos; Niger. **Dahomey:** Agouagou. **Togo:** Adele (as Bismarckburg); Mangu; Misahöhe; Wegbe. **Ghana:** Accra; *Achimota; *Odumase; *Pong-Tamale, Northern Territories; *Somanya, Krobo. Also "Guinea" (type locality; probably Christianborg). Possibly the records from **Ivory Coast** (*fide* Chabanaud) and **Sierra Leone** (*fide* Jan) belong here, but no scale counts are available.

*Range.* Southern Nigeria west to Ghana, and probably Ivory Coast possibly even as far as Sierra Leone.

### Prosymna frontalis (Peters)

1867b. *Temmorhynchus frontalis* Peters (part). Monatsb. Akad. Wiss. Berlin, p. 236, pl —, figs. 1-1d: Otjimbingue, Southwest Africa.
1894a. *Prosymna frontalis* Boulenger, p. 248.
1898. Sclater, p. 99.
1910b. Boulenger, p. 508.
1910. Lönnberg, p. 5.
1910b. Sternfeld, p. 20, fig. 21.
1910c. Sternfeld, p. 55.
1912. FitzSimons, F. W., p. 88.
1916g. Chabanaud, p. 439.

1929a. Werner, p. 142.
1955a. Mertens, p. 94.
1902. *Prosymna* (*Pseudoprosymna*) *bergeri* Lindholm, in Lampe, Jahrb. Nassau. Ver. Naturk. (Wiesbaden), **55**, p. 57: Rietmond, Gibeon District, Southwest Africa.
1910b. Boulenger, p. 509.
1910b. Sternfeld, p. 20, fig. 21.
1912. FitzSimons, F. W., p. 88.
1914b. Methuen & Hewitt, p. 143.
1915c. Werner, p. 360.
1916g. Chabanaud, p. 439.
1929a. Werner, p. 142.
1938. FitzSimons, V. F., p. 156.

Further citations of "*frontalis*" will be found under *s. bivittata*, *lineata* and *m. laurenti*.

*Common Name.* Southwest African Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single prefrontal; frontal large; loreal as long as high; preocular 1; postoculars 2, rarely 1[149]; temporals 1 + 2; upper labials 6-7, the third and fourth entering the orbit; lower labials 8-9, the first 3, rarely 4, in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 160[150]-188 (♂♂ 160[150]-169; ♀♀ 180-188); anal entire; subcaudals 34-51 (♀♀ 34-38; ♂♂ 48-51).

*Color.* Above, head light gray finely dusted with black, a more or less distinct dark crossband along the posterior margin of the prefrontal, or between the eyes, and a dark crescentic blotch on the parietals which may be reduced to an interparietal streak or spot; except for a black subocular spot, sides of head and neck whitish; a broad black nuchal band followed by several similar crossbands that become progressively fainter and ill-defined posteriorly; body and tail gray to pale yellowish brown on the sides, each scale edged with pale purplish brown or blackish, their centers often whitish and forming wavy whitish crossbands. Below, white, yellowish white, or brown, uniform.

*Size.* Length of a ♂ (T.M. 17597) 187 (153 + 34) mm.; the *bergeri* cotype ♂ (Wies.Mus.) 160 (131 + 29) mm.; the *bergeri*

[149] On one side only of the holotype.

[150] 150 for a Usakos ♂ (*fide* Werner:1915c) requires verifying.

cotype ♀ (Wies.Mus.) 155 (135 + 20) mm.; the *frontalis* holotype ♂ (Berlin Mus.) 300 (244 + 56) mm.[151]; largest ♀ (S.M.F. 46739) 355 (312 + 43) mm., from Kaiser-Wilhelms-berg.

*Remarks.* The ventrals and subcaudals of the type have been recounted by Dr. H. Wermuth and found to be 162 (not 167) and 48 (not 50) respectively; actually 48 conforms to Peters' illustration.

The name *frontalis* had fallen into disuse for 25 years until revived by Mertens (1955) whose detailed reasons for synonymizing *bergeri* should be consulted. Actually, though by a different route, I had arrived at the same conclusion in 1950 when the following paragraph was written, though unpublished until now.

*P. bergeri* was based on two snakes in which the posteriorly directed nasal suture was incomplete; such was also the case with a Klipfontein snake taken by FitzSimons (1938). In all other respects — both of lepidosis and color pattern — they conform so closely to *frontalis* that one can only conclude the character is a variable one or that Peters' figure is incorrect in this detail.

*Localities.* **Little Namaqualand:** Klipfontein. **Southwest Africa:** Churutabis; Gobabis; Kaiser-Wilhelms-berg near Okahandja; Narudas Sud at 4800 feet; Okahandja; Otjimbingue; Rietmond; Usakos.

*Range.* Little Namaqualand north to Southwest Africa.

### Prosymna angolensis Boulenger

1873b. *Prosymna frontalis* Bocage (not Peters), p. 218.
1882a. Bocage (part: omit Angoche = *lineata*), p. 288.
1895a. Bocage, p. 98, pl. xi, fig. 2.
1896d. Boulenger, p. 641.
1915a. *Prosymna angolensis* Boulenger, Proc. Zool. Soc. London, p. 209: based on Bocage, 1895a, which see for description. No type locality so Huila, 15°5′S., 13°30′E., Angola is now designated.
1916g. Chabanaud, p. 439.
1929a. Werner, p. 142.
1937b. Monard, pp. 114, 122.

[151] As remeasured by Dr. Wermuth, Peters' figures were obviously erroneous, they read: "Totallange 0m135; Schwanz 0m057."

1955a. Mertens, p. 94.
1937b. *Prosymna ambigua* Mertens (not Bocage), p. 13 (Cubal).
1938e. *Prosymna ambigua ambigua* Mertens (not Bocage), p. 439.

For another citation of "*angolensis*" see under *a. ambigua*.

*Common Names.* Southwest Angola Shovel-snout (A.L.); *golongo* (in Caeonda: Bocage).

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single prefrontal; frontal large; loreal rhomboidal or pentagonal; preocular 1; postocular 1-2; temporals 1 + 2; upper labials 6, the third and fourth entering the orbit; the first 3 lower labials in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals "145-163" (*fide* Bocage: probably ♂♂ 145-155; ♀♀ 155-163); anal entire; subcaudals "17-25" (*fide* Bocage: probably ♀♀ 16-19; ♂♂ 25-28).

*Color.* Above, head yellowish brown, with or without black spots of which the most common is a black band across the frontal anteriorly, followed by a pair of black blotches on the supraoculars and parietals; a black nuchal spot or collar more or less distinguishable on the paler yellowish-brown specimens, followed on the back by two longitudinal series of round, black or blackish, spots; sometimes uniform, or each scale with a light spot near its tip and the edges of the scales somewhat darker. Below, including the lips and two or three outermost scale-rows, yellowish white.

*Size.* Largest recorded, presumably a ♀ (Bocage:1873b), 360 (331 + 29) mm.; next largest ♀ (Mertens:1938e), 327 (305 + 22) mm. from Cubal.

*Remarks.* No type for *angolensis* was designated by Boulenger, whose basis was "*frontalis* Bocage (1895:not of Peters)" in Herp. Angola Congo, p. 98, pl. xi, fig. 2. Bocage lists his material as coming from seven localities in the high plateau of Benguella and Mossamedes. Mertens (1955, p. 94) errs in giving Duque de Braganca, northwest Angola, as type locality for *angolensis*, for this was type locality of *ambigua* Bocage (cf. p. 100).

Mertens (1955) suggests the possibility of *angolensis* being a race of *frontalis* from which it is chiefly distinguished by its much lower ventral and subcaudal counts — so much lower, in fact, that the gap is unlikely to be bridged. More probably its relationship lies with *lineata* Peters of Mozambique, with which it is connected by Southern Rhodesian material.

*Localities.* **Southwest Africa:** Karakuwisa, Okawango. **Angola:** Biballa; Caconda; Cubal; Ebanga; Huila; Maconge (Maconja); Mossamedes; Quibula; Quindumbo; Quissange.

*Range.* Southwest Africa north to southwest Angola.

### Prosymna ambigua ambigua Bocage

1866a. *Prosymna meleagris* Bocage (not Reinhardt), p. 47.
1873b. *Prosymna ambiguus* Bocage, Jorn. Sci., Lisboa, **4**, p. 218: Duque de Braganca, Angola.
1895a. *Prosymna ambigua* Bocage, p. 99, pl. xi, figs. 1a-d.
1896d. Boulenger, p. 641.
1910. Lönnberg, p. 6.
1915a. Boulenger, p. 208.
1915e. Boulenger, p. 625.
1929a. Werner, p. 142.
1931. Monard, p. 104.
1937b. Monard (part), pp. 114, 123.
1910. *Prosymna meleagris concolor* Lönnberg, Arkiv. Zool., **7**, No. 8, p. 5, fig. 2: Mukimbungu, Lower Congo River, Belgian Congo.
1916g. Chabanaud, p. 440.
1940. *Prosymna angolensis* Bogert (part:not Boulenger), p. 59 (Capelongo).
1941a. *Prosymna ambigua ambigua* Uthmöller (part), p. 43.
1950f. Laurent, p. 129.
1953a. Laurent, pp. 21, 23.
1953. Witte, p. 206, fig. 65.
1954b. Laurent, p. 52.
1956. Laurent, p. 193.
1952b. *Prosymna ambigua bocagei* Laurent (part:not Boulenger), p. 200 (for ♀ with 154 ventrals, substitute Leopoldville for "Nepoko, Uele").
1953a. *Prosymna ambigua loveridgei* Laurent, p. 23 (no description: "un seule specimen, du Mayombe").
1954b. Laurent, Serv. Cult. Comp. Diam. Angola. Museu Dundo, No. 23, p. 56, fig. 15: Boma, Lower Congo River, Mayombe, Belgian Congo.

Of the foregoing citations several are actually "in part"; further listings of "*ambigua*" will be found under *m. laurenti*, *angolensis*, *a. bocagii*, *a. urundiensis*, *a. brevis* and *a. stuhlmanni*.

*Common Name.* Northwest Angola Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge[152]; separated by the single bandlike internasal from the single prefrontal; frontal large; loreal longer than high; preocular 1; postoculars 2, rarely 1[153]; temporals 1 + 1, 1 + 2 or 2 + 2[154]; upper labials 5-8,[155] rarely the second and third, or second, third and fourth, normally the third and fourth, entering the orbit; lower labials 7-8, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15-17[156] rows; ventrals[157] 129-154 (♂♂ 129-140; ♀♀ 145-154); anal entire; subcaudals 19-34 (♀♀ 19-24; ♂♂ 26-34).

*Color.* Above, rostral and upper lip white; each parietal with or without a whitish spot; a broad black nuchal collar sometimes present; otherwise head and body gray, pale brown or black, the apex of each scale with or without a whitish spot. Below, yellowish white to blackish gray, uniform, or the center of each ventral with a more or less distinct dusky mark, the edges of each scute paler.

*Size.* Largest ♂ (R.G.M.G. —), 283 (237 + 46) mm.; largest ♀ (R.G.M.G —), 345 (313 + 32) mm., both from Bokoro (ex. Laurent:1954b). The type of *ambigua,* evidently a ♀, was given as 225 (113 + 12) mm. The type of *loveridgei*, also a ♀, was given as 313 (281 + 32) mm.

*Remarks.* In the synonymizing of *m. concolor* from the Lower Congo with *a. ambigua* from northwest Angola, Laurent (1954b) and I are in complete accord. It seems somewhat illogical, how-

[152] The rostral is fused with the internasal in some Bokoro snakes; in others the internasal is fused with the prefrontal (Laurent:1954b).

[153] One on left side only of Kamina and Mushishi ♂♂ (Laurent:1954b).

[154] 2 + 2 on one side of a Hemptinne St. Benoit ♂; in another specimen the second lower temporal is fused with the fifth upper labial (Laurent:1954b).

[155] From 5-8 in Laurent's material; 5, the second and third entering the orbit in the type of *concolor* as well as in one of Laurent's specimens.

[156] 17 in the types of *ambigua* and *concolor;* both 15 and 17 present from Bokoro; Kununga and Leopoldville examined by Laurent (1954b).

[157] 131-140 in Laurent's ♂♂, but 129 for a Vila da Ponte snake (*fide* Monard:1931) which requires checking; also the color description given by Monard suggests the possibility that he had an *angolensis* as a second specimen.

ever, to then postulate the presence of two races in the Lower Congo by describing *a. loveridgei* from there. *P. a. loveridgei,* as Laurent points out, differs from all other Congo *Prosymna* seen by him in that the horizontal suture, that normally extends backwards from the nostril to the loreal, is, in *loveridgei,* connected by a vertical fissure to the first labial. This has resulted in the splitting off of a small supplementary nasal.

On the left side of one (I 3598) of the 50 Liwale *a. stuhlmanni* I examined, there is no horizontal suture whatever, the nostril being in an entire nasal. As long ago as 1923 Schmidt recorded the creation of a supplementary loreal by vertical fissuring of the loreal in one of his Garamba *a. bocagii.* Since then other instances of fissuring have been reported among members of this genus so that it seems reasonable to assume that the only known example of *a. loveridgei* is nothing more than an aberrant *a. ambigua.*

Apart from its small supplementary shield, the only way in which *a. loveridgei* ♀ differs from ♀ ♀ of *a. ambigua* is in having 24 (as against 19-21) subcaudals. Other more adequately represented species and races of *Prosymna* display an even wider range than the 6 which would result from extending the range from 19 to 24 so as to include *a. loveridgei.* It would appear that I am destined to outlive my namesake which, regretfully, I must consign to the synonymy.

*Dentition.* Maxillary teeth 8, followed by 3 enlarged, lancet-shaped teeth, according to Bogert (1940: dealing with a Capelongo ♀), who points out that "the anterior part of the maxilla makes a diagonal suture with a posterior elongation of the premaxilla," apparently an unusual adaptation calculated to provide mechanical support for the snout during burrowing operations.

Laurent (1954b), dealing with Congo material, reports the maxillary teeth as 8, the first six small, the last 2 enlarged. In this he sees a difference with "*angolensis,*" to which species Bogert had referred the Capelongo snake which I believe to be an *a. ambigua.*

*Sexual dimorphism.* In addition to the marked difference in the number of ventrals and subcaudals, as may be seen in the *Description*, 15 ♂♂ (measured by Laurent) have tails included in H. & B. 4.6 to 5.8[158] times; 13 ♀♀ (9 + 1 measured by Laurent) have tails included in H.& B. 8.6 to 10.7 times.

*Localities.* **Angola:** Capelongo (Bogert:1940); Duque de Braganca (type of *ambigua*); *Missao di Dondi (M.C.Z. 32468); Vila da Ponte.[158] **Belgian Congo:** Albertville; Bokoro; Boma (type of *loveridgei*); Bukena; Congo da Lemba; Hemptinne St. Benoit, Kasai; Kalina; Kamina; Kilwezi; Kisantu; Kunungu; Leopoldville; Lomami; Mabwe; Mayombe; Mukimbungu (type of *concolor*); Mushishi; Ndwa; Thysville; Tipoyo, Fiji Territory; Upper Katanga. **French Congo:** *Brazzaville.

*Range.* Northwest Angola, north through Belgian Congo to French Congo.

### Prosymna ambigua bocagii Boulenger

1897b. *Prosymna bocagii* Boulenger, Ann. Mag. Nat. Hist., (6) **19**, p. 278, figs. —: Zongo, Ubangi Rapids, Belgian Congo.
1901g. Boulenger, p. 9, pl. iii, fig. 4.
1903b. Bocage, p. 63.
1906c. Mocquard, p. 467 (but omit *Vassei* as syn.).
1910. Lönnberg, p. 6.
1915a. Boulenger, p. 208.
1916g. Chabanaud, p. 440.
1929a. Werner, p. 142.
1937c. Loveridge, p. 275.
1908. *Aparallactus concolor* Werner (not Fischer), (1907), p. 1882 (text).
1916f. *Prosymna ambigua* Chabanaud (not Bocage), p. 372.
1916g. Chabanaud, p. 439.
1919g. Boulenger, p. 25 (*Prosymna*).
1923. Schmidt, p. 89, figs. 7-8 (but "♀" is a ♂).

[158] 6.5 times in one of Monard's (1931) Vila da Ponte snakes, if his measurements (195 + 30) mm. are correct. The assignment of his two specimens to *ambigua* should be checked for the scale counts (ventrals 129; subcaudals 26), though not the locality, agree with *a. brevis*. The coloration, however, seems to be that of *angolensis*. It might be translated as follows: Above, gray; prefrontal with a black, V-shaped marking extending to above the eyes as in *frontalis*, from the frontal across the parietals to the post-parietal scales extends a large nuchal blotch; body reticulated with black, on the dorsum a double row of black, sometimes confluent, spots tend to be more symmetrical posteriorly (Monard:1931). The low number of ventrals rule out the possibility of these Vila da Ponte snakes being referred to either *angolensis* or *frontalis*.

1933m. Witte (part), p. 91.
1936. *Prosymna ambigua stuhlmanni* Pitman (part:not Pfeffer), p. 126, pl. viii, figs. 1-2; col. pl. H, fig. 2 (Uganda records).
1938a. Pitman (part) p. 310.
1938b. Pitman (part), pp. 39, 120-121, 149, 310, pls. as above.
1952b. *Prosymna ambigua bocagei* Laurent, p. 200.
1954b. Laurent, p. 54.
1956. Laurent, p. 193.
1956c. *Prosymna ambigua ambigua* Loveridge (not Bocage), p. 45 (9 in reprint).

*Common Name.* Northeast Congo Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge; separated by the single band-like internasal from the single prefrontal, which occasionally may enter the orbit[159]; frontal large; loreal as long as,[160] or longer than, high; preocular 1, rarely absent[161]; postoculars 1, 2 or 3[162]; temporals 1 + 1, 1 + 2 or 2 + 2[163]; upper labials 5-7, rarely the second and third,[164] normally the third and fourth, entering the orbit; lower labials 7-8, the first 3, rarely 4, in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 139-168 (♂♂ 139-148; ♀♀ 161-168); anal entire; subcaudals 17-32 (♀♀ 17-21; ♂♂ 27-32).

*Color.* Above dark brown, head uniform, body seemingly paler owing to the center of each scale being lighter (blue gray), imparting a reticulate appearance which extends to the outermost rows. Below, blackish brown, each ventral and subcaudal shield with a median, transverse, light bar.

*Size.* Largest ♂ (A.M.N.H. 12145) 298 (250 + 48) mm., from Garamba; largest ♀ (R.G. 3381) 398 (366 + 32) mm., from Niangara; the holotype ♀ (R.G. 44) was 347 (320 + 27) mm. as remeasured by Laurent (1954b).

*Remarks.* See comments under *P. a. urundiensis* Laurent.

[159] On one side of *bocage* type and in a Batangafo ♀ (A.N.S.P. 20763).

[160] A small supplementary loreal is split off from nasal in a Garamba ♂ (not ♀ :A.M.N.H. 12144).

[161] In the Lado snake mentioned by Werner (1908), if referable to *bocagii*.

[162] Three in a Nopoko River ♂ reported by Laurent (1954b).

[163] Both 1 + 1 and 1 + 2 occur in the Sudan and Uganda; 2 + 2 in an Avakubi ♂ (Laurent:1954b).

[164] Asymmetrically in a Congo snake (Laurent:1954b).

*Hemipenis.* Schmidt (1923), when figuring the extraordinary unforked hemipenis of this species with its single sulcus, remarks that the organ is at least 10 mm. longer than the tail and in consequence must be "telescoped" when withdrawn. He suggests that the tail reduction responsible for this unusual condition has resulted from the adoption of burrowing habits.

*Sexual dimorphism.* In addition to the marked difference in the number of ventrals and subcaudals, as may be seen in the *Description*, in 8 known ♂♂, tail is included in H. & B. length 5.1 to 6.8 times; in 7 known ♀♀, tail is included in H. & B. length 11.0 to 12.8 times.

*Breeding.* On July 2, at Molongori, a ♀ held 6 eggs measuring about 16 to 23 x 7 mm.

*Localities.* **Sudan:** *Molongori; *Torit. **Uganda:** *Eastern Province; Lado = West Nile Province; Serere, Teso. **Belgian Congo:**[165] Avakubi; Garamba; Karawi, Ubangi; Mahagi Port; Nepoko, Uele; Niangara; Upper Ubangi; Zongo, Ubangi Rapids (type). **French Congo:** ? Batangafo.

*Range.* Southern Sudan and Uganda, west through northern Belgian Congo to French Equatorial Africa.

### Prosymna ambigua urundiensis Laurent

1933j. *Prosymna ambigua* Witte (not Bocage), p. 123.

1953a. *Prosymna ambigua urundiensis* Laurent, p. 23 (no description: "un seule specimen de Nyanza").

1954b. Laurent, Serv. Cult. Comp. Diam. Angola. Museu Dundo, No. 23, p. 56: Nyanza on Lake Tanganyika, Belgian Ruanda-Urundi.

1956. Laurent, p. 193.

*Common Name.* Urundi Shovel-snout (A.L.).

*Description* (adapted from Laurent). Preocular 1; postoculars 2; temporals 1 + 2; upper labials 6, the third and fourth entering the orbit; lower labials 8-9, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 152 (in ♂); anal entire; subcaudals 32 (in ♂).

*Size.* Length of holotype ♂ (R.G.M.C. 9232) 235 (199 + 36) mm.

[165] Omitted are a ♂ and ♀ (I.R.S.N. 4885) allegedly from Mpese-Inkisi, Lower Congo, listed in a footnote by Laurent (1954b) who regards data as doubtful.

*Remarks.* That the sexing is correct seems certain from the 32 subcaudals, the same number as present in a *P. a. bocagii* ♂ (C.N.H.M. 58405) from as far north as Torit in the Sudan. The only grounds for the separation of *urundiensis,* therefore, rest on its possession of 152 ventrals (139-148 in ♂ ♂ *bocagii*). A range of 10 in ♂ ventrals is also found in *a. ambigua, a. brevis, frontalis* and *m. laurenti,* but is exceeded in half a dozen other *Prosymna.* If the range of *a. bocagii* is extended to include *urundiensis* it would give a range of 14 ventrals as opposed to an acceptable range of 16 in ♂ ♂ of the much better known *a. stuhlmanni.* Further collecting of *Prosymna* in Urundi should indicate which is the correct course to follow.

### Prosymna ambigua brevis Laurent

1950f. *Prosymna ambigua ambigua* Laurent (not Bocage), p. 129.
1953. Witte (part), p. 206 (Sandoa).
1954b. *Prosymna ambigua brevis*, Laurent, Serv. Cult. Comp. Diam. Angola, Museu Dundo, No. 23, p. 50, figs. 12-14: Dundo, Angola.

*Common Name.* Northeast Angola Shovel-Snout (A.L.).

*Description* (after Laurent). Preocular 1; postoculars 1-2; temporals 1 + 2, fused in one specimen, the second temporal fused with the fifth upper labial in another; an additional upper labial is asymmetrically present in two snakes; lower labials 8-9, the first 3 or 4 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 127-146 (♂ ♂ 127-136; ♀ ♀ 140-146); anal entire; subcaudals 15-30 (♀ ♀ 15-17; ♂ ♂ 25-30).

*Color.* For comments on its variability, see Laurent (1954b).

*Size.* Length of ♂ (R.G.M.C. 7929) 308 (267 + 41) mm.; length of ♀ (R.G.M.C. 8276) 351 (325 + 26) mm., both from Sandoa.

*Remarks.* In ventral counts this form overlaps those of *a. stuhlmanni,* but is apparently distinguishable by the low number of subcaudals in the ♀. In ♂ ♂, however, the subcaudal ranges overlap so that a specimen of *a. stuhlmanni* from Abercorn (M.C.Z. 54081) with 139 ventrals and 29 subcaudals might be referred to *a. brevis* were it not for the accompanying ♀ (M.C.Z. 54082) having 155 ventrals and 20 subcaudals. For further comments on the status of this form, see Laurent (1954b).

*Sexual dimorphism.* The relationship of tail to total length is given by Laurent (1954b) as ranging from .075 to .087 in ♀♀, and from .146 to .150 in ♂♂.

*Localities.* **Angola:** Dundo; Sombo. **Belgian Congo:** Sandoa, Katanga.

*Range.* Northeast Angola, north to southeast Belgian Congo.

### Prosymna ambigua ruspolii (Boulenger)

1896b. *Asthenophis ruspolii* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2) **17**, p. 12: Magala, Umberto Id., Ganale Doria, Somalia.
1897g. Boulenger, p. 279.
1915d. Boulenger, p. 649.
1927. Calabresi, p. 54.
1929a. Werner, p. 143.
1930e. Scortecci, p. 18.
1949a. Parker, p. 65.
1929e. *Prosymna agrestis* Scortecci, Atti Soc. Ital. Sci. Nat. (Milano), **68**, p. 272, figs. —: Villaggio Duca degli Abruzzi, Somalia.
1939a. Scortecci, p. 273.
1949a. Parker, p. 63.

*Common Name.* Southern Somaliland Shovel-snout.

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single prefrontal; frontal large; loreal longer than high; preocular 1; postocular 1; temporals 1 + 2; upper labials 6, the third and fourth entering the orbit; lower labials 8, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 130-154 (♂♂ 130-136; ♀♀ 143-154); anal entire; subcaudals 23-27 (♀♀ 23-?; ♂♂ 32-37).

*Color.* Above, dark reddish to purplish brown; usually a light spot on the apex of each scale, whose free edge may appear lighter. Below, yellowish gray, somewhat darker anteriorly.

*Size.*

Length of ♂ (type of *ruspolii*) 198 (165 + 33) mm.,

length of ♀ (type of *agrestis*) 252 (226 + 26) mm., length of largest assumed ♀ (Scortecci: 1929a) 295 (262 + 33) mm.

*Remarks.* As pointed out by Parker (1949a, p. 63), there is nothing to distinguish *agrestis* from *ruspolii* except the alleged

differences in dentition, and he suggests that the enlarged posterior maxillary teeth have been overlooked in the juvenile type of *Asthenophis*, and the second example of *ruspolii*, which Scortecci called a ♀, is almost certainly a ♂. Parker rightly urges a re-examination of the dentition of these two specimens, but, as my attempt to borrow one of the cotypes met with no response, I venture to risk censure by synonymizing *agrestis* with *ruspolii*.

*Breeding.* One 295 mm. ♀ from Belet Amin held 4 eggs, each measuring "275 [presumably 27.5] x 7 mm." (Scortecci:1939a).

*Localities.* Somalia: Belet Amin; Jonderma; Magala; Villaggio Duca degli Abruzzi.

*Range.* Somalia.

### Prosymna ambigua ornatissima Barbour & Loveridge

1928c. *Prosymna ornatissima* Barbour & Loveridge, Mem. Mus. Comp. Zool., **50**, p. 120, col. pl. ii, fig. 2: Nyange, Ulugnru Mountains, Tanganyika Territory.
1928j. Loveridge, p. 75.
1937f. Loveridge, p. 502.
1941a. Uthmöller, p. 40.

*Common Name.* Ornate Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single prefrontal; frontal large; loreal longer than high; preocular 1; postoculars 0-1-2; temporals 1 + 2 (the anterior one entering the orbit below the postocular on the right side of M.C.Z. 23270 only); upper labials 6, the third and fourth entering the orbit; lower labials 7-8, the first 3 in contact with the single pair of sublinguals; midbody scales smooth, in 15 rows; ventrals 127-150 (♂♂ 127-132; ♀ 150); anal entire; subcaudals 27-40 (♀ 27; ♂♂ 35-40).

*Color.* Above, rostral and rest of head scarlet (whitish in alcohol) except for a black crossband over the prefrontal-frontal suture (frequently reduced to a vertical streak from eye to labials), and an arrow-shaped extension of the black body coloring reaching to the frontal; body black with 13 or 14 irregularly transverse, scarlet crossbars which may be interrupted on the vertebral line or broken and alternating. Below, throat pink; rest of undersurface black except where the lateral scarlet blotches impinge on the outer edges of the ventrals.

No other member of the genus is so handsomely and aposematically colored (*vide* plate).

*Size.* Length of paratype ♂ (M.C.Z. 23272) 297 (242 + 55) mm.; length of holotype ♀ (M.C.Z. 23271) 286 (252 + 34) mm.

*Breeding.* On October 4, the umbilical ventral scutes of a young 143 (117 + 26) mm. male were still unhealed.

*Habitat.* A forest-edge species occurring from 2000 to 2500 feet. For further details see original description.

*Localities.* **Tanganyika Territory:** Uluguru Mountains—Nyange; Vituri.

*Range.* Tanganyika Territory.

### Prosymna ambigua stuhlmanni (Pfeffer)

1891a. *Prosymna ambigua* Boulenger (not Bocage), p. 306.
1894a. Boulenger, p. 248.
1896a. Bocage, p. 93.
1896. Tornier, p. 71 (reprinted 1897).
1897. Tornier, p. 65.
1902b. Boulenger, p. 17.
1907a. Boulenger, p. 11.
1908b. Boulenger, p. 229.
1910b. Boulenger (part), p. 509 (omit Angola).
1910a. Sternfeld, p. 21, fig. 23.
1912. FitzSimons, F. W., p. 88.
1923c. Loveridge, p. 880.
1924b. Loveridge, p. 5.
1928c. Barbour & Loveridge, p. 121.
1933h. Loveridge, p. 244.
1934. Pitman, p. 295.
1893. *Ligonirostra Stuhlmanni* Pfeffer, Jahrb. Hamburg Wiss. Anst., **10**, p. 78, pl. i, figs. 8-10: Usambara, Tanganyika Territory.
1906b. *Prosymna Vassei* Mocquard, Bull. Mus. Hist. Nat. (Paris), **12**, p. 250: Mozambique.
1906c. Mocquard, p. 467.
1916g. Chabanaud, pp. 433, 440, figs. 1-2.
1917e. Chabanaud, p. 225, fig. — (correcting previous drawing).
1909e. *Prosymna variabilis* Werner, Jahres. Ver. Nat. Württemberg, **65**, p. 57: Moshi, Tanganyika Territory.
1910a. Sternfeld, p. 21.
1915c. Boulenger, p. 626.
1916g. Chabanaud, p. 438.

1924b. Loveridge, p. 6.
1929a. Werner, p. 142.
1909c. *Stenorhabdium temporale* Werner, Jahres. Ver. Nat. Württemberg, 65, p. 60: "East Africa."
1929a. Werner, p. 164.
1915c. *Prosymna bocagii* Boulenger (part:not Boulenger:1897b), p. 625.
1924b. Loveridge, p. 5.
1936j. *Prosymna ambigua stuhlmanni* Loveridge, p. 254.
1936. Pitman (part), p. 126, pl. viii, figs. 1-2; col. pl. H, fig. 2 (omit Uganda records).
1937f. Loveridge, pp. 493, 496.
1938a. Pitman (part), p. 310.
1938b. Pitman (part), pp. 39, 120-121, 149, 310, pls. as above (reprint: omit Uganda records).
1939. Someren, p. 155.
1941. Moreau & Pakenham, p. 108.
1941a. Uthmöller, pp. 26, 43.
1941b. Uthmöller, p. 235.
1942e. Loveridge, p. 281.
1950. Ionides, p. 101.
1951. Battersby, p. 829.
1951a. Loveridge, p. 192.
1953e. Loveridge, p. 265.
1955e. Loveridge, p. 184.
1937. *Prosymna ambigua bocagii* Uthmöller (not Boulenger:1897b), p. 110.

*Common Name.* East African Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single, rarely divided,[166] prefrontal; prefrontal very rarely entering orbit[167]; frontal large; loreal as long as, or longer than, high; preocular 1, rarely absent[168]; postoculars 2, rarely 1[169] or absent[170]; temporals

166 Divided in a juvenile ♀ (U.M.M.Z. 61221) found bottled at Morogoro, but without locality (Loveridge: 1932e).

167 Entering in type of *rassei*, also in occasional specimens at M.C.Z.

168 Absent on one side only of an Ngatana ♂ (M.C.Z. 40562), and a Lumbo ♂ (M.C.Z. 18203).

169 One on 9 sides only of 80 snakes examined.

170 Absent through fusion with supraocular on right side of a Liwale ♀ (M.C.Z. 51311).

rarely 1 + 1,[171] usually 1 + 2, occasionally 1 + 3[172] or 2 + 2[173]; upper labials 5-7, rarely the second and third or second, third and fourth, normally the third and fourth, entering the orbit[174]; lower labials 7-8, the first 3, rarely 4, in contact with the single pair of sublinguals. Midbody scales smooth, in 15 rows; ventrals 129-155 (♂♂ 129-144; ♀♀ 144-155); anal entire; subcaudals 19-34 (♀♀ 19-28; ♂♂ 29-34).

*Color.* Above, rostral and upper lip yellowish white, otherwise head and body gray (young), each scale edged with darker, or plumbeous (adult), uniform or with two dorsolateral rows of white flecks. Below, usually white, uniform or with irregular dusky markings which may form a median line along the tail, rarely brown or black.[175]

Battersby (1951), after examining 38 East African *a. stuhlmanni* (together with 2 Uganda snakes which I refer to *a. ambigua*), found that 26 had a more or less distinguishable dorsolateral series of white specks on either flank, but no trace of such markings in the more southwesterly material extending into Northern Rhodesia. He decided this speckling was uncorrelated with age, sex or scale-counts. The seeming geographical difference I believe to be fortuitous.

*Size.* Length of ♂ (M.C.Z. 40562) 238 (200 + 38) mm., from Ngatana, largest ♀ (M.C.Z. 54082) 323 (293 + 30) mm. from Abercorn, surpassing even a ♀ (B.M. 1902.2.12.91) of 280 (250 + 30) mm., from Mazoe. It would appear that there is an increase in size in the Rhodesias as one approaches the range of the somewhat larger typical race.

*Remarks.* Mocquard (1906c) erroneously synonymized his *vassei* with *bocagii*. Chabanaud (1916g) corrected Mocquard's miscounts of ventrals and subcaudals, but himself published a

[171] 1 + 1 through fusion of the lower temporal with fifth upper labial on left side o fa Mapenya ♀ (M.C.Z. 40560).

[172] 1 + 3 on 3 sides of 2 Liwale ♀♀ (M.C.Z. 51395, 51397).

[173] 2 + 2 on right side of an Abercorn ♂ (M.C.Z. 54081).

[174] In the respective ratios of 2-2-74.

[175] In one (M.C.Z. 51390) of 18 Liwale snakes, and two (M.C.Z. 54081-2) Abercorn specimens (♂♀).

figure in which only two labials (later amended) entered the orbit. In 1918 I collected (M.C.Z. 18203) a normal *stuhlmanni* from within three miles of the type locality of *vassei*.

After examining the ♀ cotype of *variabilis* Werner, I (1933h) synonymized it with *stuhlmanni* as the character on which it was based is a juvenile one.

If the holotype of *Stenorhabdium temporale*, whose shrivelled condition rendered Werner's examination of it "distinctly difficult," was indeed procured in "Ostafrika" by student Schwarzkopf, there can be little doubt it was based on an aberrant ♂ *a. stuhlmanni*. I have never seen a specimen in which the parietal was in contact with the labial, which might be brought about by fusion of the temporals with labials, but I have recorded fusion of the lower temporal with the fifth labial in a Ngatana snake, also a "Morogoro" reptile in which the internasal was divided. In Werner's type both internasal and prefrontal were allegedly divided; possibly this appearance may have resulted from the shrivelled condition of which Werner complains. In other respects his holotype, now lost I believe, conforms to a male *a. stuhlmanni* in its lepidosis and scale counts.

*Breeding.*

On May 28, at Mapenya nr. Witu, a ♀ held 3 eggs measuring 20 x 6 mm.

On November 23, at Liwale, T.T. a ♀ held 3 eggs measuring 30 x 7 mm.

Others on January 5 and February 23 from this locality also held large eggs.

*Diet.* Young geckos (*Hemidactylus mercatorius*, possibly *mabouia*) were present in the stomachs of a Liwale and a Mtimbuka snake.

*Habitat.* Uthmöller (1937) has taken this species from a grass-grown heap of stones in a coffee plantation. I caught two that had been ploughed up by a tractor working in a sisal plantation; others were found beneath the rotting roots of a fallen tree; beneath a rotting log; under a bundle of rotting grass on the mud veranda of a hut; and in a termitarium. They occur from the coastal plain to upland savanna at 5500 feet in the Chyulu Hills.

*Localities.* **Kenya Colony:** Chyulu Hills; *Mapenya; *Mkonumbi; Mombasa; *Ngatana. **Tanganyika Territory:** *Amboni Estate near Tanga; *Bagamoyo; Bukoba[176]; Dar es Salaam; Gomberi; *Kilwa; Litumba; *Liwale; Malimba; Masasi; "? Morogoro"; Moshi; *Mpwapwa; Mto-wa-Mbu; *Tunduru; Usambara (type of *stuhlmanni*). **Zanzibar. Mozambique:** *Kasumbadedza; *Lumbo; Mozambique. **Nyasaland:** *Mtimbuka; Shire Valley. **Northern Rhodesia:** *Abercorn; Mbala Region, East Loangwa District. **Southern Rhodesia:** *Imbezi, Mtali; Mazoe; Salisbury. **Transvaal** (eastern): Hectorspruit; Letaba. **Zululand:** Gwalileni; *Hluhluwe; Ingwavuma; Kosi Bay; Ubombo.

*Range.* Coastal region of Kenya Colony, south to Zululand, Natal, northwest through the Rhodesias to ? Bukoba,[176] Tanganyika Territory.

### Prosymna ambigua transvaalensis Hewitt

1910b. *Prosymna transvaalensis* Hewitt, Ann. Transvaal Mus., **2**, p. 73: Tzaneen, Zoutpansberg District, Transvaal.
1916g. Chabanaud, p. 440 (key).
1929a. Werner, p. 142 (key).

*Description.* Preocular 1, *rarely 2* (T.M. 5200 only); postocular 1 rarely 2 (T.M. 5200 only), but in the type the single preocular is fused with the supraocular on the right side; temporals 1 + 2 or *2 + 3* (*not* 1 + 3) on one side (of T.M. 5200); upper labials 5-6, the second and third or second, third and fourth, entering the orbit (both conditions present in T.M. 5202) except in one paratype (T.M. 5200) where they are separated from the eye by suboculars; lower labials 7-9, the first 3, rarely 4 (on one side of T.M. 5201), in contact with the single pair of sublinguals which, with their following scales in no way differ from those of *a. stuhlmanni*. Midbody scales smooth, in 15 rows; ventrals 155-158; anal entire; subcaudals 22-25 (*not* 26).

*Color.* Above, black, with two interrupted dorsolateral flecks, none on the tail. Below, white.

*Size.* Length of type ♀ (T.M. 10120) 260 (235 + 25) mm.

*Sexual dimorphism.* In the two adults, of which the type has been sexed by Dr. FitzSimons and corollary evidence suggests the

[176] West of Lake Victoria so possibly referable to *P. a. ambigua*.

other also is a ♀, the tail is contained in the head and body length from 7.5 to 9.4 times.

*Remarks.* I am indebted to Dr. V. F. FitzSimons, Director of the Transvaal Museum, for all the preceding information not included in the original scanty description. From the above it will be seen that, excepting for some aberrations (given in italics) in one of the young paratypes (T.M. 5200) from Medingen, this alleged race differs only from *a. stuhlmanni* in its slightly higher ventral counts of 155-158 (144-155 in *stuhlmanni* ♀ ♀). Both ventrals and subcaudals suggest that all four specimens are ♀ ♀.

I consider they represent a small pocket of individuals for Tzaneen is on the railway just south of the Beit Bridge across the Limpopo from Southern Rhodesia where *P. a. stuhlmanni* occurs. Medingen lies slightly east of Tzaneen; only a little farther east again *a. stuhlmanni* has been obtained at Letaba and ranges south to Zululand.

There are no westerly records until we come to *P. a. ambigua*. It is on this account that I have allowed the name to stand for the present, though it appears possible it will eventually have to be synonymized with *a. stuhlmanni* and the range of ventrals of that form extended upward to 158.

*Localities.* **Transvaal:** Medingen, Klein Letaba River (3 paratypes); Tzaneen (type).

*Range.* Northern Transvaal.

### Prosymna jani Bianconi

1862. *Prosymna Janii* Bianconi, Mem. Accad. Sci. Ist. Bologna, (2) 1. p. 470, pl. i (*Ianii* on plate): Inhambane, Mozambique.
1862? Bianconi, p. 386, pl. xv (reprint of above).
1862. Jan, **2**, p. 56.
1876. Jan, pl. ii, fig. 1.
1882a. Peters, p. 106.
1884a. Rochebrune, p. 151 (ignored).
1894a. Boulenger, p. 249 (*jani;* so spelled by most subsequent authors).
1896a. Bocage, p. 100.
1908b. Boulenger, p. 229.
1910b. Boulenger, p. 509.

1910. Lönnberg, p. 5.
1912. FitzSimons, F. W., p. 88.
1916g. Chabanaud, p. 438.
1929a. Werner, p. 142.

*Common Name.* Keel-scaled Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single prefrontal; frontal large; loreal longer than high; preocular 1; postoculars 2-3; temporals 1 + 2; upper labials 6-7, the third and fourth entering the orbit; lower labials 8, the first four in contact with the sublinguals. Midbody scale-rows 15-17 (15 in Kosi Bay snake, said to be 17 in Inhambane type) keeled; ventrals 113-119; anal entire; subcaudals 30-37.

*Color.* Above, head yellowish, a black crossbar on the prefrontal extends backwards over frontal to unite with a black area covering parietals and nape, except for a light cordiform patch on nape; body pale reddish brown with a double series of conspicuous black spots along the anterior two-thirds of the back. Below, yellowish-white, uniform.

*Size.* Length of holotype (ex Bianconi) 180 (148 + 32) mm., from Inhambane; length of another (Brit. Mus.) 224 (188 + 36) mm., from Kosi Bay. Both likely to be males.

*Remarks.* Nothing in the bibliography adds anything to the original descriptions of Bianconi and Jan, which are frequently in disagreement. Ventrals are given as 117 and 119 for the holotype, subcaudals as 32 and 37. When Peters (1882a) gave the latter as 34 he was perhaps trying to strike an average. Though both give the scale-rows as 17, Jan adds that they are reduced to 15 posteriorly. There are certainly only 15 in the Kosi Bay snake which I have examined, and I suspect that the count of 17 was made in advance of midbody. Only these two examples of this handsome little species are known.

*Localities.* **Mozambique:** Inhambane. **Natal:** Kosi Bay, Zululand.

*Range.* Southeast coast of Mozambique (23°S.) to northeast corner of Natal (28°).

### Prosymna pitmani Battersby

1951. *Prosymna pitmani* Battersby, Ann. Mag. Nat. Hist., (12) **4**, p. 828: Kilwa, Southern Province, Tanganyika Territory.
1955c. Loveridge, p. 184.
1957a. Loveridge p. 11.

*Common Name.* Multi-scaled Shovel-snout (A.L.).

*Description.* Rostral with angular horizontal edge; separated by the single bandlike internasal from the single prefrontal; prefrontal narrowly excluded from orbit; frontal large; loreal usually wedge-shaped, longer than high; preoculars 1-2; postoculars 2; temporals 1 + 2 or 2 + 2; upper labials 6, the third and fourth entering the orbit; lower labials 8, the first 3 in contact with the single pair of sublinguals. Midbody scales smooth, in 19-21[177] rows; ventrals 140-157 (140-151[178] in ♂♂; 155-157 in ♀♀); anal entire: subcaudals 17-27 (17-20 in ♀♀; 25-27 in ♂♂).

*Color.* Above, rostral and upper lip more or less yellowish white, the labials blotched with darker; otherwise head, body and tail purplish black (dark gray when about to slough), each scale, except the outermost on either side, with a whitish terminal spot. Below, including the lower part of each lateral scale, white, uniform.

*Size.* Length of holotype ♂ (B.M. 50.1.3.96) 309 (275 + 34) mm., from Kilwa; length of ♀ (M.C.Z. 54527) 308 (285 + 23) mm., from Liwale.

*Remarks. Prosymna pitmani*, distinguished from all other members of the genus by its 19-21 midbody scale-rows, appears to be ancestral to *P. a. stuhlmanni*.

*Hemipenis.* Battersby comments on the extremely large size of the retractor muscles which, lying in many convolutions, extend from the hemipenis to almost the tip of the tail. In the paratype, evagination of the right hemipenis had resulted in the convolutions being straightened out and the muscles so extended that they are almost threadlike. Similar conditions were noted in *P. ambigua stuhlmanni*, *P. somalica* and *P. meleagris*, but not in ♂♂ of *P. s. sundevallii* whose retractor muscles were quite straight.

[177] 19 in 5 ♂♂ and 1 verified ♀ : 21 in the remaining 5 ♀♀ in M.C.Z.

[178] 151 in holotype ♂ *fide* Battersby.

*Breeding.* On June 6, at Liwale, a ♀ held 4 eggs measuring 8 x 20 or 23 mm.

*Diet.* The stomach of the aforementioned ♀, as also of the largest ♀ taken in May, each held two or more, 30 mm. long, collapsed shells of hatched-out snake or lizard eggs! This is our sole information of the diet of this species so recently discovered by C. J. P. Ionides.

*Localities.* **Tanganyika Territory:** Kilwa; Liwale; Mavuji River (upper reaches in western part of Kilwa District); Nanguale (type locality in Kilwa District, Mr. Ionides informs me).

*Range.* Southeastern Tanganyika Territory.

## Genus CHILORHINOPHIS Werner

1907. *Chilorhinophis* Werner, Akad. Anz., Wien, **44**, p. 479 (brief notice), and 1908 (for 1907), Sitzb. Akad. Wiss. Wien, **116**, p. 1881 (59 in reprint). Type by original designation: *C. butleri* Werner.

1927. *Parkerophis* Barbour & Amaral, Bull. Antivenin Inst. America, **1**, p. 25. Type by original designation: *Apostolepis gerardi* Boulenger.

1927b. Parker, Ann. Mag. Nat. Hist., (9) **20**, p. 84.

*Definition.* Maxillary very short, with 3-4 teeth followed after an interspace by a pair of large grooved fangs situated below the anterior border of the eye, posterior end of maxilla horseshoe-shaped; a maxillary-ectopterygoid foramen; ectopterygoid simple; palatine and sometimes pterygoid teeth present; mandibular teeth slightly enlarged posteriorly. Head small, not distinct from neck; snout rounded, not prominent; eye small, with round or vertically subelliptic pupil; nasal entire, separate from or fused with first labial; no internasals; no loreal; preocular present or absent; usually no anterior temporal.

Body cylindrical, elongate; scales smooth, without apical pits, in 15 rows; ventrals rounded; anal divided. Tail short, obtuse; subcaudals paired. Hemipenis of male with sulcus spermaticus unforked. Hypapophyses absent posteriorly in the vertebral column.

*Range.* Central and eastern Africa, viz. Sudan, south through eastern Belgian Congo to Southern Rhodesia, northeast through Mozambique to southern Tanganyika Territory.

*Remarks.* Boulenger (1913b, p. 104) expressed the opinion that nothing in the dentition or sealation of *gerardi* justified its separation from the South American genus *Apostolepis.*

Barbour and Amaral (1927, p. 25), without African material and overlooking Werner's description, stated that the African snakes should be separated as *Parkerophis,* characterized by (1) a smaller head, (2) smaller gape, (3) 4 instead of 6 labials, (4) the complete separation of nasal from preocular by the prefrontal forming a suture with the second labial. As a similar arrangement to that described for this last character is exhibited by specimens of the Brazilian *A. assimilis* and *A. dorbignyi* (both represented in the collection of the Museum of Comparative Zoology at that time), the argument is invalid. The first two differences are merely relative, being based on the smaller size of the African species, so that little is left but their third character — a poor one indeed for the erection of a genus.

However, Parker (1927b, p. 84), discovering the similarity of the ectopterygoid foramen of *Parkerophis* to that of related species, while differing structurally from the foramen occurring in *Apostolepis* and its neotropical allies, concluded that the external similarities between the genera were convergencies rather than the result of phylogeny. He therefore supported the separation proposed by Barbour and Amaral, though on more substantial grounds.

Battersby (1950, p. 415) reviewed the genus and, unjustifiably I think, synonymized *carpenteri* with *butleri.*

### *Key to the Species*

1. Nasal shield distinct from first labial; prefrontal separated from orbit by preocular; frontal about 1½ times as long as broad . . . . . 2
   Nasal shield fused with first labial to form a single nasolabial shield[179]; prefrontal either entering orbit or separated from it by preocular; frontal only slightly longer than broad . . . . . 3

2. Ventrals in ♂♂ 308-310, in ♀ 375; subcaudals in ♂♂ 25-26, in ♀ 23; tail included 17.8-18.6 times in total length of ♂♂, 23.6 times in ♀; maximum recorded length of ♂ 486 mm., of ♀ 569 mm.; range:

[179] Not fused on right side of a ♀ (M.C.Z. 51328) from Liwale, the only one of about 50 paratypes to show such a reversion to the ancestral arrangement.

western Tanganyika Territory (Ujiji) south to Northern Rhodesia (Nyamkolo), west to southern Belgian Congo (Lokonzolwa, Lake Mweru) . . . . . *g. tanganyikae* (p. 170)

Ventrals in ♂♂ 263-294, in ♀♀ 274-348; subcaudals in ♂♂ 27-31, in ♀♀ 20-26; tail included 12.3-15.2 times in total length of ♂♂, 16.2-21.2 times in ♀♀; maximum recorded length of ♂ 424 mm., of ♀ 513 mm.; range: southern Belgian Congo south to Southern Rhodesia . . . . . *g. gerardi* (p. 172)

3. Ventrals in holotype ♂ 256; subcaudals 33; tail included 10.4 times in total length of ♂; length of only known ♂ 313 mm.[180]; range: Sudan (Mongalla) . . . . . *butleri* (p. 174)

Ventrals in ♂♂ (unknown for *c. carpenteri*) 217-238, in ♀♀ 216-270 (or 288); tail included 10.5-12.9 times in *c. liwalensis* ♂♂, 14.4-19.6 in ♀♀ (both races); maximum recorded length of *c. liwalensis* ♂♂ 300 mm., of ♀♀ 335 mm. . . . . 4

4. Three longitudinal dark stripes along back and sides; range: south eastern Tanganyika Territory (3 or 4 localities) . . . . . *c. liwalensis* (p. 175)

Five longitudinal dark stripes along back and sides; range: eastern Mozambique (Ancuabe, about 30 miles west of Porto Amelia) . . . . . *c. carpenteri* (p. 177)

### Chilorhinophis gerardi tanganyikae Loveridge

1933h. *Chilorhinophis gerardi* Loveridge (part), p. 262.
1934. Pitman, p. 298.
1937f. Loveridge, p. 496.
1937. Pitman (part), p. 330 (Nyamkolo only).
1938b. Pitman (part), p. 183 (Nyamkolo only).
1947. Witte & Laurent (part), p. 54, figs. 43-45.
1951a. *Chilorhinophis gerardi tanganyikae* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 195: Nyamkolo, Lake Tanganyika, Northern Rhodesia.
1953. Witte, p. 263.

*Common Names.* Western Tanganyika Two-headed Snake (English); *kasimwanamatenga* and *kalambanzila* (Kirungu).

*Description.* Rostral twice as broad as deep, the portion visible from above as long as one third of its distance from the frontal; nostril in a single nasal that is *not* fused with the first labial; prefrontals longer than broad, not entering the orbit; frontal longer

[180] Not 315 mm. says Dr. J. Eiselt, who kindly sexed the only known specimen and corrected a number of errors in the original description.

than its distance from the rostral, 1⅓-1½ times as long as broad, 1¼-2 times as broad as a supraocular, its length included 1½-1¾ times in that of a parietal; preocular 1, moderate; eye small, its diameter two-thirds its distance from the mouth; postocular 1, moderate; a moderate to large posterior temporal; upper labials 4, second in contact with a prefrontal, third entering the orbit, fourth largest and in contact with a parietal; lower labials 5, the first broadly in contact with its fellow behind the mental, 3 labials in contact with the anterior sublinguals, which are divergent and longer than the posterior.

Midbody scales smooth, in 15 rows; ventrals 308-375 (♂♂ 308-310; ♀ 375); anal divided; subcaudals 23-26 (♀ 23; ♂♂ 25-26).

*Color in alcohol.* Above, head and neck black, the black descending on the sides of the neck suggesting a collar; labials yellow with black spots on rostral, beneath eye, and near gape; prefrontals, parietals and nape each bearing two small white spots; back yellowish white with a dark brown vertebral stripe flanked by a dark brown dorsolateral stripe on the fifth row and adjacent halves of the fourth and sixth scale-rows, the three stripes extending almost to tip of tail; the three lower lateral scale-rows uniform white; posterior third of tail black with lighter flecking. Below, throat and belly immaculate yellowish white, a black crossband on posterior third of tail, whose tip is also black. For color in life see Loveridge (1933h).

*Size.* Larger ♂ (M.C.Z. 48434) 486 (460 + 26) mm., tail being included in total length of ♂♂ 17.8-18.6 times; only known ♀ (I.G. 15.824) 569 (545 + 24) mm., its tail being included in total length 23.6 times. Midbody diameters in ♂♂ 4.5-5 mm., of ♀ about 3.5 mm.

*Remarks.* See Loveridge (1951a, p. 196).

*Defense.* When wriggling along, this snake applies its head to the ground while carrying its tail, which bears a striking resemblance to the head, upraised as if prepared to defend itself in a rearguard action. (Loveridge: see also Mertens, 1946b, pp. 31, 71).

*Habitat.* This slender species inhabits dry savanna both at Ujiji and Nyamkolo, where the type was found by men engaged in clearing weeds from the road leading to the London Missionary

Society's station on the bluff overlooking the bay. At the time the countryside was very dry, the rains having ceased a month previously.

*Localities.* **Tanganyika Territory:** Ujiji; also reported by natives as occurring at Kasanga. **Northern Rhodesia:** Nyamkolo. **Belgian Congo:** Lukonzolwa, Lake Mweru (Moeru).

*Range.* Tanganyika Territory (in the vicinity of Lake Tanganyika) and Northern Rhodesia, northwest to the Belgian Congo (in the vicinity of Lake Mweru).

### Chilorhinophis gerardi gerardi (Boulenger)

1913b. *Apostolepis Gerardi* Boulenger, Revue Zool. Afr., **3**, p. 103, fig. —: Kikondja, Lualaba District, Belgian Congo.
1915a. Boulenger, p. 214.
1925. Werner (1924), p. 149.
1928i. Witte, p. 9.
1927. *Parkerophis gerardi* Barbour & Amaral (part), p. 25.
1927b. Parker, pp. 81, 82, 84, fig. 1.
1933m. Witte, p. 95.
1933h. *Chilorhinophis gerardi* Loveridge (part: citations only), p. 262.
1937. Pitman (part), **4**, pp. 329, 330.
1938b. Pitman, pp. 182, 183.
1943a. Witte & Laurent, p. 157.
1947g. Laurent, p. 39.
1947. Witte & Laurent (part: omit some citations), p. 54, figs. 43-45.
1950. Battersby, p. 417.
1953. *Chilorhinophis gerardi gerardi* Witte, p. 261, fig. 90.
1956. Laurent, p. 152.

*Common Name.* Congo Two-headed Snake (English).

*Description.* Rostral broader than deep, the portion visible from above as long as 1/4 to 2/5 its distance from the frontal; nostril in a single nasal that is *not* fused with the first labial; prefrontals longer than broad, not entering the orbit; frontal longer than its distance from the rostral, 1 2/5 to 2 times as long as broad, 1 1/4 to 1 4/5 times as broad as a supraocular, its length included 1 1/4 to 1 1/2 times in that of a parietal; preocular 1, moderate; eye small, its diameter equal to its distance from the mouth; postocular 1, moderate; a large (rarely 2) upper temporal bordering the parietal; upper labials 4, second in contact with a prefrontal, third (divided in one specimen) entering the

orbit, fourth largest and in contact with a parietal; lower labials 5, first broadly in contact with its fellow behind the mental, 3 labials in contact with the anterior sublinguals, which are divergent and longer than the posterior.

Midbody scales smooth, in 15 rows; ventrals 263-348 (♂♂ 263-294; ♀♀ 274-348); anal divided; subcaudals 20-31 (♀♀ 20-26; ♂♂ 27-31).

*Color in alcohol.* Above, head and neck black, the black descending on the sides of the neck suggesting a collar; labials speckled with yellow below and behind the eye; back yellowish with a black vertebral stripe and a dark dorsolateral stripe on the fifth and adjacent halves of the fourth and sixth scale-rows; posterior third of tail pale blue irregularly blotched with black. Below, throat immaculate white, belly and anterior portion of tail yellowish, the posterior third bluish flecked with black and white.

*Size.* Total length of type ♂ (R.G.M.C. 1205) 315 (290 + 25) mm.; largest ♂ (R.G.M.C. 11588) 424 (392 + 32) mm., tail being included in total length of ♂♂ 12.3-15.2 times; largest ♀ (R.G.M.C. 748) 513 (486 + 27) mm., tail included in total length of ♀♀ 17.2-22.2 times.

The measurements, and consequently proportions, of the largest ♂ furnished by Witte & Laurent (1943a, p. 158; 1947, p. 55) are amended in a letter from de Witte (25.xi.49).

*Dentition.* Maxillary, palatine and pterygoid teeth of a Sinoia snake have been figured by Parker (1927b).

*Hemipenis.* Not bifurcate; basal spines larger but relatively less numerous; it is possible to distinguish about 4 series of large spines intermingled with spines only half as big; in the more dilatable part of the organ there are about 40 spines arranged in 7 or 8 chevrons, being most minute and numerous towards the tip, which extends to the fifteenth caudal (Laurent:1956).

*Localities.* **Belgian Congo:** Elisabethville; Kankunda, Luapula River; Kaswabilenga, Lufiri River; Kikondja, Lualaba District; Kisantu, Lower Congo District; Lofoi, Upper Katanga District; Lukafu, Upper Katanga District; Lukulu, Tanganyika District; Mabwe, Lake Upemba; Mukabe-Kasari, Lualaba District; Tshilunda Village, Lualaba District. **Northern Rhodesia:**

(N.M.S.R.—C.I. 43.1.2.: Miss Wilson coll. 1923. Seen A.L.). **Southern Rhodesia:** Lukosi; Sinoia Lomagundi District.

*Range.* Southern Belgian Congo, south to Southern Rhodesia.

### Chilorhinophis butleri Werner

1907. *Chilorhinophis butleri* Werner, Akad. Anz. Wien, **44.** p. 479 (brief notice), and 1908 (for 1907), Sitzb. Akad. Wiss. Wien, **116.** p. 1881, pl. iii, figs. 8 a-d: Mongalla, Sudan.
1910a?. Sternfeld, p. 33.
1915d. Boulenger, p. 654.
1924b. Loveridge, p. 7.
1925. Werner (1924), p. 148.
1937. Pitman, **4.** p. 329, pl. xii, fig. 1; col. pl. M, figs. 1-1b.
1938b. Pitman, p. 181, pl. xii, fig. 1; col. pl. M, figs. 1-1b.
1947. Witte & Laurent, p. 56, figs. 46-48.
1950. Battersby (part), pp. 416, 417 (omit synonymy).

*Common Names.* Sudanese Two-headed Snake (English); Sudan Black-and-Yellow Burrowing Snake (Pitman).

*Description.* Rostral one and a third times as broad as deep,[181] the portion visible from above about two-fifths[182] its distance from the frontal; nostril in a single nasal that is fused with the first labial, so borders the mouth; prefrontals longer than broad, not entering the orbit; frontal shorter than the parietals; supraocular small; preocular 1; postocular 1 or absent; upper temporal large, bordering the parietal; upper labials 4 (if the nasolabial be considered the first), second in contact with a prefrontal, third entering the orbit, fourth largest and in contact with a parietal; lower labials 5, the first broadly in contact with its fellow behind the mental, 3 labials in contact with the anterior sublinguals, which are divergent and larger than the posterior pair.[183]

Midbody scales smooth, in 15 rows; ventrals 256; anal divided; subcaudals 33 pairs.

[181] Werner's statement to the contrary notwithstanding, for the rostral of the holotype has been measured with vernier callipers by Dr. J. Eiselt who (letter of 26.x.54) finds the breadth to be 1.1 mm., the depth .85 mm.

[182] Eiselt's measurement for the portion of the rostral visible from above, is .5 mm., its distance from the frontal 1.25 mm.

[183] Werner's figure of the type, by Josef Fleischmann, is in error.

*Color.* Above, head and neck black, the latter descending on the sides of the neck suggesting a collar; labials yellow; occiput unspotted; back yellowish white with a black vertebral stripe; a black dorsolateral stripe on the fifth scale-row; a black bar across tail. Below, throat and belly immaculate yellowish; on tail the dorsal black cross bar is continued to form a complete ring on the middle third, a few black spots on tip.

*Size.* Total length of holotype ♂ (Vienna Mus.) 313 (283 + 30) mm.,[184] the tail being included in total length 10.4 times. Midbody diameter 4 mm.

*Remarks.* The type was brought in dead by natives on March 30, 1905, and named after A. E. Butler, the then Game Warden of the Sudan. Being still the only known specimen, the foregoing description is based on the original one, together with information gleaned from Fleischmann's drawing, besides corrections and amendments supplied me by Dr. J. Eiselt after a careful re-examination of the type. Fleischmann's misleading figures form the basis of all subsequent illustrations.

In assuming that Sternfeld's statement (1910a) "bis 32 cm." represented the measurement of an Amani snake, Pitman (1938b, p. 138) erred, for in round figures this was the length given by Werner for the holotype. Moreover, Sternfeld's description is also based on Werner's, and is not that of the Amani snake he referred to *butleri.* This specimen has been missing from the Berlin Museum since I first enquired for it 30 years ago. I suggest it may have been a misidentified *Aparallactus werneri,* a common Amani reptile with a color pattern not unlike that of *Chilorhinophis butleri.*

*Habitat.* Presumably arid upland savanna, possibly in the vicinity of the Nile.

*Localities.* **Sudan:** Mongalla.

*Range.* Sudan (*unknown* from Uganda and Tanganyika Territory).

### Chilorhinophis carpenteri liwalensis Loveridge

1950. *Chilorhinophis carpenteri* Battersby (not Parker), p. 416.
1950. Ionides, p. 105.

[184] Sexed and carefully remeasured for me by Dr. J. Eiselt (14.ix.54).

1951a. *Chilorhinophis carpenteri liwalensis* Loveridge, Bull. Mus. Comp. Zool., **106**, p. 196: Liwale, Southern Province, Tanganyika Territory.

1955e. Loveridge, p. 188.

*Common Names.* Eastern Tanganyika Two-headed Snake (English); *kitandamba,* i.e. the one found among *ndandamba* beans (Ngindo, but not specific).

*Description.* Rostral nearly twice as broad as deep, the portion visible from above as long as about two times its distance from the frontal; nostril in a single nasal that is fused with the first labial, so borders the mouth; prefrontals longer than broad, entering or not entering the orbit; frontal shorter than its distance from the rostral, slightly longer than broad, about twice as broad as a supraocular, much shorter than a parietal; preocular 1, moderate, minute, or absent; eye small, its diameter about two-thirds its distance from the mouth; postocular 1; upper temporal large, bordering a parietal; upper labials 4 (if the nasolabial be considered the first), second in contact with a prefrontal, third entering the orbit, fourth largest and broadly in contact with a parietal; lower labials 5, the first broadly in contact with its fellow behind the mental, 3, rarely 4, labials in contact with the anterior sublinguals, which are divergent and longer than the posterior.

Midbody scales smooth, in 15 rows; ventrals 216-270 (♂♂ 217-238; ♀♀ 216-270[185]); anal divided; subcaudals 18-30 (♀♀ 18-24; ♂♂ 25-30).

*Color in alcohol.* Above, head and neck black, the black descending on the sides of the neck suggesting a collar; labials yellow; temporal with or without a white spot; back yellowish white, a broad brown vertebral stripe on vertebral scale and adjacent halves; a dark dorsolateral stripe on adjacent halves of the fifth and sixth scale-rows, very rarely (M.C.Z. 50090 only) the lower lateral scales may be faintly edged with brown; posterior half of tail black, except for some blue-gray mottling about the tip. Below, chin with or without dusky markings, otherwise throat

[185] 288 (verified by A.L.) in a Kilwa ♀ (Brit. Mus.) with 18 subcaudals, unless this represents an undescribed subspecies. Its inclusion would give a ventral range of 73 for ♀ *c. liwalensis*, comparable to the 74 displayed by ♀ *g. gerardi*.

and belly immaculate yellowish white; proximal portion of tail white, separated by a black bar from a blue-gray area near the tip.

In life, according to Ionides, the basic color ranges from light yellow to khaki.

*Size.* Largest ♂ (M.C.Z. 51327) 300 (274 + 26) mm., tail being included in total length of ♂ ♂ 10.5-12.9 times; type ♀ (M.C.Z. 50076) 335 (315 + 20) mm., but surpassed by another ♀ (M.C.Z. 52832) of 360 (339 + 21) mm.,[186] tail being included in total length of ♀ ♀ 14.4-19.6 times. Midbody diameter of ♀ type, 3.5 mm.

*Remarks.* See Loveridge (1951a, p. 198).

*Dentition.* Pterygoid teeth on prepared skull, 3 or 4.

*Diet.* Worm-lizards (*Amphisbaena ionidesii*) were present in the stomachs of two Liwale snakes.

*Habits. Chilorhinophis*, like adult blind-snakes, usually remains underground except following heavy rain.

*Localities.* **Tanganyika Territory:** Southern Province: Kilwa[187]; Liwale; Masasi District; Ruponda, Lindi District; Tunduru District.

*Range.* Southeastern Tanganyika Territory.

### Chilorhinophis carpenteri carpenteri (Parker)

1919. *Apostolepis gerardi* Carpenter (not Boulenger), p. 496.
1925. Carpenter, p. 132, pl. vii.
1927. *Parkerophis gerardi* Barbour & Amaral (part), p. 25.
1927. *Parkerophis carpenteri* Parker, Ann. Mag. Nat. Hist., (9) **20**, p. 85, fig. 3: "Anquabe," i.e. Ancuabe, Mozambique.
1937. *Chilorhinophis carpenteri* Pitman, 4, pp. 329-331.
1938b. Pitman, pp. 182-184 (reprint).
1947. Witte & Laurent, p. 57, figs. 49-50.

*Common Name.* Mozambique Two-headed Snake (English).

*Description.* Rostral much broader than deep, the portion visible from above as long as about 2½ times in its distance from the frontal; nostril in a single nasal which is fused with the first

[186] Also exceeded by a Kilwa ♀ (Brit. Mus.) measuring 410 (390.5 + 19.5) mm. which, however, may represent an undescribed subspecies.

[187] Unless this Kilwa ♀ proves to be subspecifically distinct. Kilwa is 125 miles northeast of Liwale.

labial, so borders the mouth; prefrontals longer than broad, entering the orbit; frontal shorter than its distance from the rostral, slightly longer than broad, twice as broad as a supraocular, much shorter than a parietal; preocular 1, minute; eye small, its diameter equal to its distance from the mouth; postocular 1, moderate; upper temporal large, bordering a parietal; upper labials 4 (if the nasolabial be considered the first), second in contact with a prefrontal, third entering the orbit, fourth largest and broadly in contact with a parietal; lower labials 5, the first broadly in contact with its fellow behind the mental, 3 labials in contact with the anterior sublinguals, which are small and subequal to the posterior.

Midbody scales smooth, in 15 rows; ventrals 269 (in only known ♀); anal divided; subcaudals 21 (in ♀).

*Color in alcohol.* Above, head and neck black, the black descending on the sides of the neck suggesting a collar; labials yellow; occiput bearing two small white spots; back yellowish white with a ladder-like, dark brown, vertebral stripe; a dark dorsolateral stripe on the adjacent halves of the fifth and sixth scale-rows, a narrow brown lateral stripe between the third and fourth scale-rows, lower lateral scales faintly edged with brown; posterior half of tail black. Below, throat and belly immaculate yellowish white; a black bar across posterior half of tail separates off a light area near the tip.

*Size.* Total length of holotype ♀ (B.M. 1918.11.20.1) 280 (264 + 16) mm.; tail length included in total length of ♀ 17.5 times. Midbody diameter 3 mm.

*Dentition.* Pterygoid teeth absent in type (*fide* Parker).

*Defense.* The defense of this genus was illustrated by the fact that the killer of the type had been induced to strike at the tail, so closely did it resemble the head and act as a directive mark, writes Hale Carpenter, who found it lying dead in the road through the British military camp behind Port Amelia, August, 1918.

*Localities.* **Mozambique:** Ancuabe (Anquabe; Ankwabe), which is 13°02′ S., 39°55′ E.

*Range.* Mozambique.

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[188] Where a date is followed by a letter of the alphabet it indicates that during the year cited the author in question published more than one paper on African herpetology. The letter has chronological significance in a more comprehensive bibliography of African Herpetology (1880-1953) which it is hoped may be published in the not too-distant future.

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Museum of Comparative Zoology and
Woods Hole Oceanographic Institution

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## No. 2 — *Four New Rajids from the Gulf of Mexico*[1]

By Henry B. Bigelow and William C. Schroeder

Museum of Comparative Zoology and
Woods Hole Oceanographic Institution

Recent otter trawling operations of the U. S. Fish and Wildlife Service vessel "Oregon" in the Gulf of Mexico have yielded four new species of batoids, three of them falling in the genus *Raja* and one in *Cruriraja*. These, added to about a dozen new species of elasmobranchs described from the Gulf during the past seven years, and records of others previously unknown from the western Atlantic, emphasize the richness of the Gulf fauna. We are indebted to Stewart Springer and Harvey R. Bullis, Jr. of the U. S. Fish and Wildlife Service for the opportunity of describing these species. Drawings are by Eugene N. Fischer.

### Raja oregoni sp. nov.

Figures 1, 2

*Study Material.* Mature male, 1440 mm in total length, holotype, U. S. Nat. Mus. No. 156710, and an immature male 1069 mm in total length, paratype, M. C. Z. No. 39617, both from the northern part of the Gulf of Mexico, the holotype from Lat. 29°10′N, Long. 88°13′W, in 205 fathoms, "Oregon" station 1247, the paratype from Lat. 28°32′N, Long. 86°20′W, in 260 fathoms, "Oregon" station 1277.

*Distinctive Characters.* The combination of features distinctive for *oregoni* among hard-nosed skates of the genus *Raja* are: anterior contour of disc deeply concave, with narrowly projecting snout, of the shape pictured in Figure 1; upper surface of pectorals without conspicuous markings of any sort; disc, rearward of the spiracles, without any large thorns, its midbelt bare even of prickles; tail with three rows of large close-set thorns extending to base of first dorsal fin; lower surface with pore openings in head region marked conspicuously with black dots.

[1] Contribution No. 932 from The Woods Hole Oceanographic Institution.

*Comparison with previously known species.* It is only with species sharing the diagnostic features listed in the preceding section that comparison seems called for, a limitation welcome

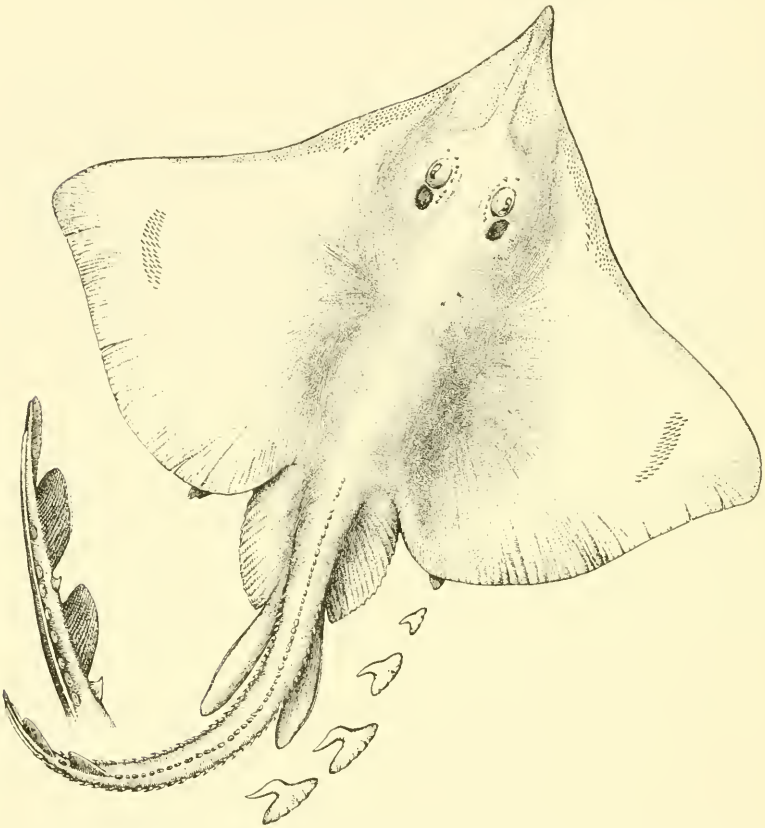

Figure 1. *Raja oregoni,* dorsal view of type, mature male 1440 mm long; end of tail showing dorsal fins and caudal fin about x 0.2; tail thorns from mid row about x 1.

because about 110 recognizably distinct species of the genus *Raja* have been named already from one part of the oceans or another (Bigelow and Schroeder 1953, p. 147).

Among the skates known from the North Atlantic (including the Gulf of Mexico) *oregoni* most nearly resembles *laevis* Mitchill 1817, the common barn-door skate of the northeastern American

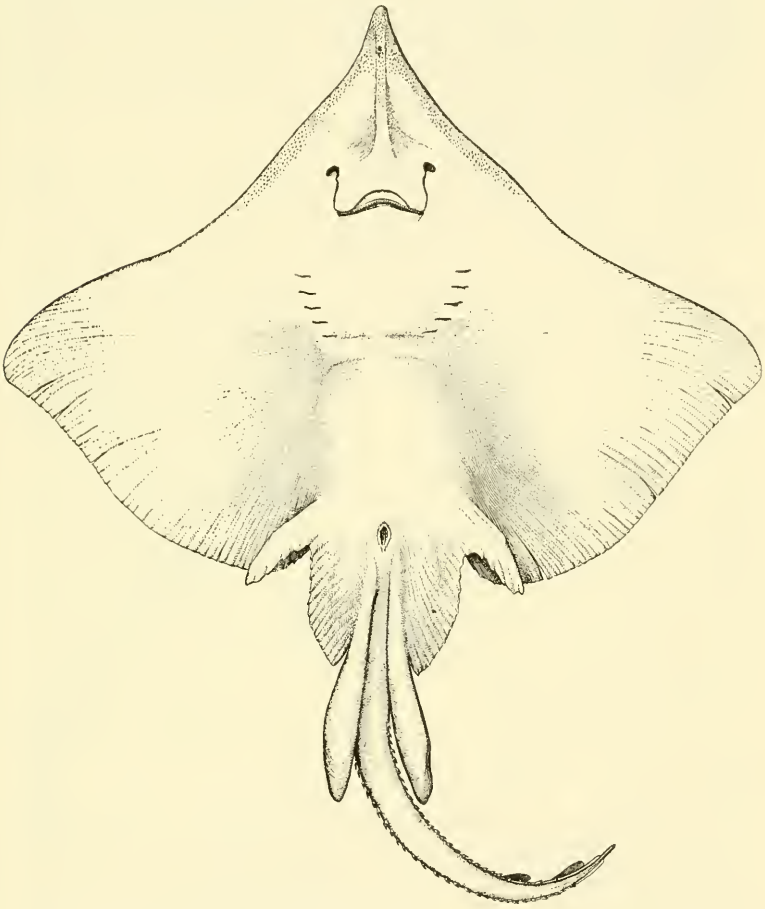

Figure 2. *Raja oregoni,* ventral view of specimen shown in Figure 1.

coast and its eastern Atlantic representative, *batis* Linnaeus 1758. But the thorns on the tail of *oregoni* are much larger than on *laevis* or on *batis,* closer set, and with those on the lateral rows

along the rear half of the tail directed rearward in very characteristic shape (Fig. 1). Other differences are that the snout is noticeably longer in *oregoni* (length anterior to orbits about 4 times as great as the distance between orbits) than in either *laevis* or *batis* (2.4-3 times) in males of about equal size; that the rostral cartilage is narrower and that the black pore markings of the ventral surface are restricted to the area anterior to the abdominal region whereas in *laevis* and in *batis* they are present on the rearward part of the disc as well.

The only other western North Atalntic skates that *oregoni* resembles at all closely in general appearance, combined with thorn pattern, are *R. olseni* Bigelow and Schroeder 1951 and *R. teevani* Bigelow and Schroeder 1951 but there is no danger of confusing it with either of these. Conspicuous respects in which it differs from *olseni* are in a shorter interspace between first and second dorsal fins, with only 1 thorn (3-6 thorns in *olseni*); in a larger number (31 to 48) of thorns in the mid-row on tail (only 13-26 in *olseni*) with the lateral rows closely and regularly spaced (irregularly and widely spaced in *olseni*). Other differences of perhaps equal significance taxonomically, though less noticeable, are that in *oregoni* the expanded outer-posterior margin of the nostrils is smooth edged (fringed in *olseni*, Bigelow and Schroeder 1951, fig. 2B; 1953, fig. 54 a B), that the upper surface of the snout, with the outer-anterior edge of the pectorals, is prickly (smooth in *olseni*), that the nuchal region is naked in *oregoni* but is armed with a strong thorn in large specimens of *olseni*[1] (not, however, on the juveniles). On the other hand, no trace is to be seen on the upper surface of *oregoni* of the white dots marking the pores that are a conspicuous feature of *olseni*, nor has the latter any dark dots on the under surface as is the case in *oregoni*.

*Oregoni* resembles *teevani* closely in anterior contour of its disc but differs in having 3 rows of prominent thorns on the tail (one row on *teevani*), by having a tail which narrows posteriorly as is usual among skates (on *teevani* the posterior half of tail is as wide or wider than the anterior), and by having a space, occupied by a thorn, between its dorsals (dorsals are confluent on *teevani*), and *teevani* lacks dark pores on the under surface.

[1] Specimens at hand include a nearly mature male *olseni* 510 mm long recently collected by "Oregon" in the Gulf of Mexico at Station 1514.

*Oregoni* is set apart, by the combination of characters classed above as "diagnostic," from all hard-nosed skates yet known

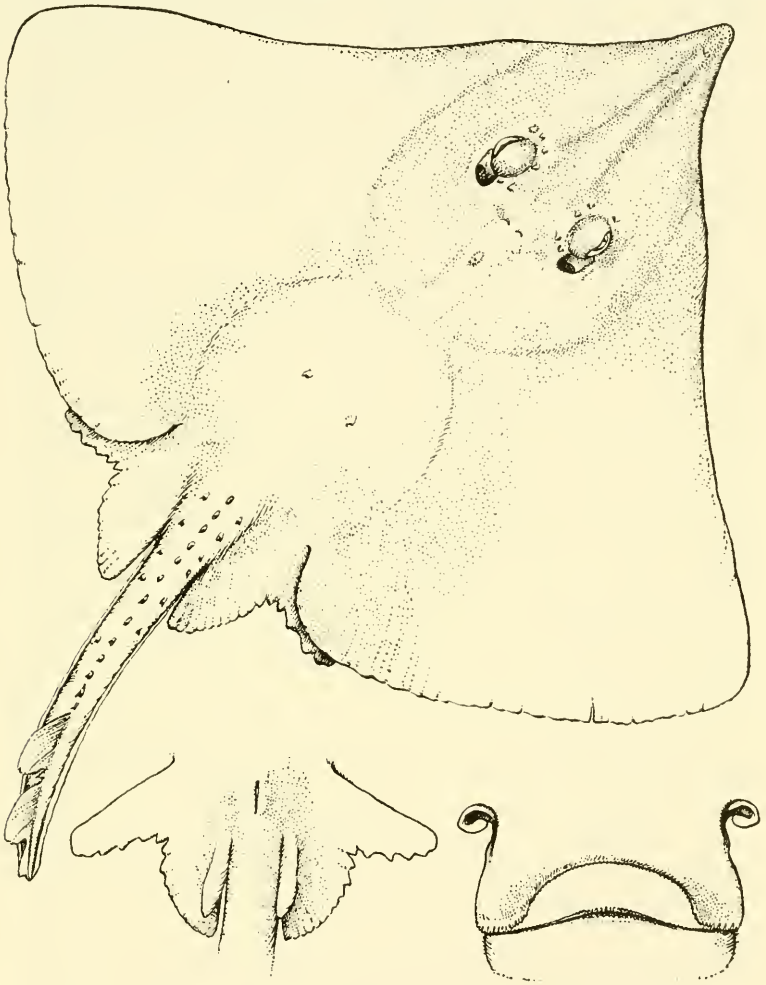

Figure 3. *Raja flavirostris,* immature male 374 mm long, "William Scoresby" station 79, from Lat. 51°01′30″S, Long. 64°59′30″W, in British Museum (Natural History); pelvic fins about x 0.4; mouth, nostrils and nasal curtain about x 0.8.

from the east coast of South America, or from the Magellanic region, with the exception of *R. flavirostris* Philippi 1892 the recorded range of which extends from Argentine and Patagonian waters to Chile. And it differs sharply from half grown and larger *flavirostris*[1] in a conspicuously longer tail (46-50 per cent of total length contrasted with 41.8-42.5 per cent in the half-grown *flavirostris* with which we have compared it; in lacking the large nuchal thorn that is characteristic of *flavirostris;* also in the greater size, more regular spacing, and shape of the thorns in the lateral rows on the tail (cf. Fig. 1 with Fig. 3 of *flavirostris*).

The only skates known from European or tropical west African waters, and from southern Africa, with which *oregoni* shares an outer anterior contour of the shape pictured in Figure 1, combined with a disc that is wholly bare of thorns posterior to the spiracles, but a tail that is armed with 3 regular rows (one median and two laterals) of close-set thorns, are: *Raja batis* Linnaeus 1758, *R. alba* Lacépède 1803 (including *R. marginata* Lacépède 1803, partly grown specimens and some adults), and *R. miraletus* Linnaeus 1758 (some specimens). And it is marked off from all of these by characters that cannot reasonably be credited to variation (whether individual or regional) or explained away on the basis either of sex or of the stage of growth of the particular specimens that have served as the bases for published accounts. Thus it differs from *batis* in the same respects in which it differs from *laevis* of the North American coast (p. 00), and this also applies to the skate that has been reported as *batis* from South Africa (Thompson 1914, p. 156; Barnard 1925, p. 70; Smith 1949, p. 66) though available information regarding the latter is scanty. And while it resembles *alba* of European waters and the skate that has been reported under that name in southern African waters from Walfish Bay on the west around the Cape to Natal on the east, first by von Bonde and Swart (1924, p. 5) both as *alba* and as *stabuliforis*

[1] We are indebted to the British Museum for the loan of three *flavirostris,* a male 374 mm long, a female 353 mm, and a juvenile male of 180 mm. from the series reported upon and pictured by Norman 1937, p. 13, fig. 4.

Garman 1913, next as *marginata* (Barnard 1925, pp. 63, 65), and more recently as *alba* by Smith (1949, p. 66), the skin of the tail of *oregoni* is naked between the thorns (described as "strongly spinulose" for *alba* by Clark, 1926, p. 48), as well as over the inner-posterior parts of the disc as a whole while it is more or less prickly on adults of *alba*. Further, the mid-row of thorns on its tail does not extend forward on to the disc as it does in *alba,* when adult, and the black pore markings characteristic of the lower surface of *oregoni* (Fig. 4) are not present on *alba*. Again, *oregoni* resembles *R. miraletus* in its pointed snout, smoothness of posterior part of disc and presence of 3 rows of thorns on the tail. But its outer anterior contour is much more deeply concave than that of *miraletus;* it lacks the 2 nuchal thorns characteristic of the latter; the number of thorns in each of the rows along is tail is much greater, there being about 50 in the median row on the male pictured in Figure 1, contrasted with 14 pictured by Rey for an adult male of *miraletus* 402 mm long, and 25 recorded by him for a female, not counting those between the dorsal fins (Rey, 1928, p. 573, pl. 13, fig. 2). Also, the interspace between the two dorsals is noticeably shorter in *oregoni* than in *miraletus;* and while black pore marks are present on the lower surface of *oregoni,* they are lacking on *miraletus*. And *oregoni* is much the larger growing member of the pair, it being unlikely that *miraletus* grows longer than about 500 mm, nor does *oregoni* show any signs of the large, light-blue centered eye spots, one of which marks the upper surface of each pectoral of *miraletus*.

It is interesting, in passing, that in the presence of the black pore markings on its lower surface *oregoni* parallels not only *batis,* but also *oxyrhynchus* Linnaeus 1758 (including *macrorhynchus* Bonaparte 1832-41) among European species. But there is no question of specific unity in this case, the snout of *oregoni* being less narrowly pointed than that of *oxyrhynchus* with the outer anterior contour of the disc much less deeply concave; the 3 rows of large tail thorns of *oregoni,* so conspicuous a feature of the adult male, being represented on the adult male *oxyrhynchus* by a single median row of about 8 to 12 thorns; the two dorsal fins separated by an interspace with a thorn in *oregoni*

being confluent at the base, or nearly so, in *oxyrhynchus;* and the black pore marks on the lower surface, which are confined

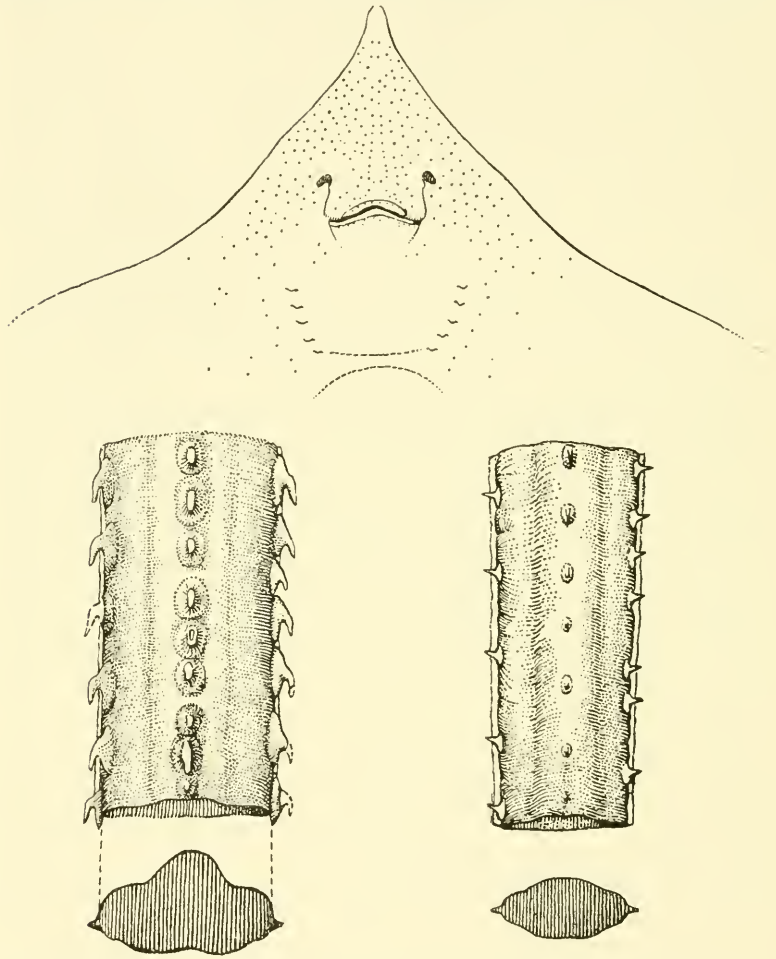

Figure 4. *Raja oregoni*, ventral view of head to show dark mucous pores, about x 0.1. *Lower left*, section of tail from 8th to 16th thorns in mid row, from first dorsal fin, about x 0.5, same specimen as in Figure 1. *Lower right*, *Raja laevis*, section of tail from 3rd to 9th thorns in mid row, from first dorsal fin, about x 0.5, a male 1185 mm long from off Nantucket, Massachusetts.

mostly to the head region in *oregoni* being distributed over the abdominal region as well in *oxyrhynchus*.

In its concave outer anterior outlines, with narrow snout, and in the black dots marking the lower surface of its head, *oregoni* most nearly resembles *R. rhina* Jordan and Gilbert 1880 among skates of the west coast of North America. But it differs from *rhina* in lacking the nuchal spine or spines that characterize *rhina*, as well as in the orderly arrangement of the thorns on its tail which on *rhina* are usually arranged irregularly with the rows interrupted. Furthermore, the mid zone of disc from the scapular region on to the tail is smooth on *oregoni* but has a band of small thorns with stellate bases on *rhina*.

Similarly, the narrowness of its "nose" combined with its lack of thorns anywhere on the disc rearward from the spiracles, contrasted with the presence of 3 rows of thorns along the tail, marks off *oregoni* among hard-nosed skates known from the Pacific coast of Central and South America, except *flavirostris* which was originally described from Chile. Respects in which it differs from *flavirostris* are summarized above.

Among the dozen or so narrow-nosed species of *Raja* that have been reported, with adequate published accounts, from the Indo-West Pacific region, three only are described, with a fourth pictured, as with the openings of the pores black-marked on the lower surface, and *oregoni* cannot be identified with any one of these. Thus *oregoni* lacks a nuchal thorn which is present and conspicuous in *australis* Macleay 1884 from Australia and Tasmania and the 3 rows of thorns on the tail of *oregoni* are longer and more regular than in *australis*. While *oregoni* lacks a nuchal thorn and the tail thorns are arranged in regular rows, *tobae* Tanaka 1916 from Japan has 2 thorns on the nuchal region and its 3 rows of tail thorns are irregular. *Oregoni*, lacking thorns along the midline of disc, differs from *porosa* Günther 1874, from the north Chinese coast, which has 3 or 4 conspicuous thorns in that area, and the 3 rows of thorns on the tail of *oregoni* distinguish it from *gudgeri* Whitley 1940, from Western Australia, which has but a single row as well as a much longer snout.

Neither can *oregoni* be referred to any of the other Indo-West Pacific species that it resembles at all closely in the anterior contour of its disc, for no known member of this group parallels

*oregoni* in the presence of three regular rows of large close-set thorns extending from the base of the tail rearward as far as the first dorsal fin, but combined with a total lack both of thorns and of prickles on the mid belt of the disc posterior to the spiracles. While it agrees with *macracauda* Ishiyama 1955 from Japan in shape of snout and disc and also in presence of dark pores below,[1] it differs from *macracauda* in having 3 rows of thorns on the tail (only 1 row in *macracauda*).

*Description of holotype.* Proportional dimensions in per cent of total length:[2]

Disc. — Extreme breadth 69.8; length 53.2.

Snout length. — In front of orbits 17.4; in front of mouth 18.5.

Orbits. — Horizontal diameter 2.8; distance between 4.5.

Spiracles. — Length 2.1; distance between 6.4.

Mouth. — Breadth 8.0.

Exposed nostrils. — Distance between inner ends 8.3.

Gill openings. — Length, 1st 1.4; 3rd 1.8; 5th 1.2; distance between inner ends, 1st 13.8; 5th 8.1.

First dorsal fin. — Vertical height 1.5; length of base 3.6.

Second dorsal fin. — Vertical height (damaged); length of base 3.8.

Pelvics. — Anterior margin 10.9.

Distance. — From tip of snout to center of cloaca 50.0; from center of cloaca to 1st dorsal 37.2; to tip of tail 50.0; from rear end of 2nd dorsal base to tip of tail 4.2.

Interspace between. — 1st and 2nd dorsals 1.3.

Disc nearly 1.4 times as broad as long, maximum angle in front of spiracles about 72°; anterior margins sinuous, being rather strongly concave from tip of snout to opposite orbits where they are slightly convex, hence again concave, this second concavity culminating about three-fifths the distance between tip of snout and outer corners of disc which are sharply rounded; posterior margins about straight near outer corner, then gently rounded, as is inner margin. Axis of greatest breadth about 72 per cent back from tip of snout to axils of pectorals. Tail with a

[1] Two young specimens examined by us, through the kindness of Dr. Ishiyama.

[2] The measurements from which the proportional dimensions have been calculated were taken on a horizontal line between perpendiculars at given points (see Bigelow and Schroeder 1953, fig. 1 and p. 4).

narrow lateral fold, low down on each side, beginning almost imperceptibly beyond level of tips of pelvics by a distance equal to about twice the interorbital width, widening posteriorly and continuing almost to extreme tip of tail being much the widest opposite dorsals and caudal membrane; length of tail from center of cloaca to origin of first dorsal fin 0.75 times as great, and to its tip equal to distance from center of cloaca to tip of snout.

A row of 7 or 8 small thorns along inner margin of each orbit, ending about opposite middle of spiracle. End of snout covered with coarse prickles; smaller prickles over rostral process, on translucent areas in front of orbits and in space between orbits. A band of small thorns and coarse prickles extends along edge of disc beginning rearward from tip of snout by a distance about equal to that between spiracles, and ending a little in advance of alar thorns, being coarsest in the area opposite and a little posterior to the spiracles. No thorns in the scapular region. A median row of about 48 thorns beginning on tail opposite axils of pectorals and extending to first dorsal fin, of unequal sizes, some with points directed obliquely rearward, others with points broken or worn; a row of thorns low down on each side of the median row, beginning a little in advance of tips of pelvics and ending opposite second dorsal fin, 31 on the left and 34 on the right, those with points still intact directed rearward parallel, or nearly so, to axis of tail; 1 thorn between dorsals. Alar thorns prominent, in two to four rather regular rows, 43 on left side of disc, 38 on right, rest of body, pelvics and tail smooth, including dorsal fins and skin over eyes. A short row of 9 or 10 mucous pores in nuchal region on each side, parallel to midline, at a distance from it equal to about two-thirds length of orbit, the pores not ringed with dark as conspicuously as on *garricki*. Lower surface with prickles in front of and aside the mouth, densest toward end of snout and along margins of disc where they extend rearward about one-half the distance toward outer angle of pectoral; a few minute prickles scattered on disc between mouth and fifth pair of gill openings; rest of lower surface naked.

Snout in front of orbits 6 times as long as orbit, its length in front of mouth 2.2 times as great as distance between exposed nostrils. Distance between orbits about 1.6 times as great as length of orbit. Orbit 1.3 times as long as spiracle. Nasal curtain fringed; expanded posterior (outer) margin of nostrils smooth, without fringes. Upper and lower jaws strongly arched centrally. Teeth $\frac{36}{33}$, more nearly in longitudinal rows than in quincunx, with circular or ovate base, those in upper jaw in median sector of mouth with a prominent narrow upright cusp, the adjacent teeth pointing very slightly toward corner of mouth where the cusps become low triangular; lower teeth similar.

Distance between first gill openings 1.7 times as great as between exposed nostrils; between fifth openings 0.97 times; first gill openings 1.2 times as long as fifth and about 0.2 as long as breadth of mouth. First and second dorsals similar in size and perhaps in shape (second dorsal damaged). Interspace between dorsals 0.36 times as long as base of first dorsal. Second dorsal confluent with caudal membrane. Caudal membrane base equal to first dorsal base. Pelvics deeply concave, strongly scalloped along anterior side of excavation, moderately so rearward; anterior margin 0.74 times as long as distance from its own origin to rear tip of pelvic; anterior lobe slender, including four radial cartilages besides the first stout one; posterior lobe moderately convex, with a narrowly rounded tip, extending 0.36 times the distance from axil of pectorals toward first dorsal. Claspers reaching beyond tips of pelvics by a distance equal to seven-tenths the distance from front of orbits toward tip of snout.

*Color.* Upper surface brownish, without spots or other markings. Lower surface pale bluish-gray on disc, pelvics and claspers; tail pale brown; scattered black pores anterior to abdominal region, most numerous around mouth and in front of level of mouth to near tip of snout.

The other known specimen of this species, an immature male 1069 mm long, differs in the following respects. The disc is about 1.3 times as broad as long; maximum angle in front of spiracles 70°; axis of greatest breadth 70 per cent back from tip of snout toward axils of pectorals. The tail is relatively shorter, the distance from center of cloaca to its tip being 0.85 times the distance from center of cloaca to tip of snout. Because of the relatively

shorter tail on the immature male, the snout is longer relative to total length (21.5 per cent to eye and 23.2 per cent to mouth opening, compared with only 17.4 and 18.5 per cent, respectively, for the mature male), the disc proportionately wider, and longer (76.5 per cent and 57.2 per cent, compared with 69.8 and 53.2 per cent, respectively, for the larger male). There are 5 small thorns along inner margin of each orbit and 1 or 2 immediately in front of orbit; fewer prickles on end of snout; and the anterior edge of the disc is smooth. The median row of thorns on tail numbers 31, the side rows 24 on the left and 22 on the right, these latter ending opposite first dorsal fin and there is no thorn between the dorsals. On the lower surface the prickles along the margins of disc extend rearward about three-fifths the distance toward outer angle of pectoral. The snout in front of orbits is 7 times as long as orbit, its length in front of mouth 2.5 times as great as distance between exposed nostrils. The jaws are less strongly arched and there are $\frac{38}{34}$ teeth, with low triangular cusps, only those near outer corners being slightly oblique.

The second dorsal, which is undamaged on this specimen, is similar to the first in shape but with a slightly shorter base and the interspace between the dorsals is relatively shorter, being about 0.14 times as long as the base of first dorsal. The anterior margin of the pelvic is almost as long as the distance from its own origin to rear tip of pelvic and the posterior lobe extends 0.31 times the distance from the axils of pectorals toward first dorsal. The claspers fail to reach the tips of the pelvics by a distance equal to length of fifth gill opening.

Known only from the offing of Cape San Blas, Florida, in 205-260 fathoms. Named in recognition of the fishery explorations of U. S. Fish and Wildlife Service vessel "Oregon" in the Gulf of Mexico and the Caribbean Sea.

### Raja garricki sp. nov.

Figures 5, 6, 7

*Study Material.* Mature male, 975 mm in total length, holotype, U. S. Nat. Mus. No. 156711, and another male 1019 mm in total length, paratype, M. C. Z. No. 39616, both from the northern part of the Gulf of Mexico, Lat. 28°32′N, Long. 86°20′W, in 260 fathoms, "Oregon" station 1277.

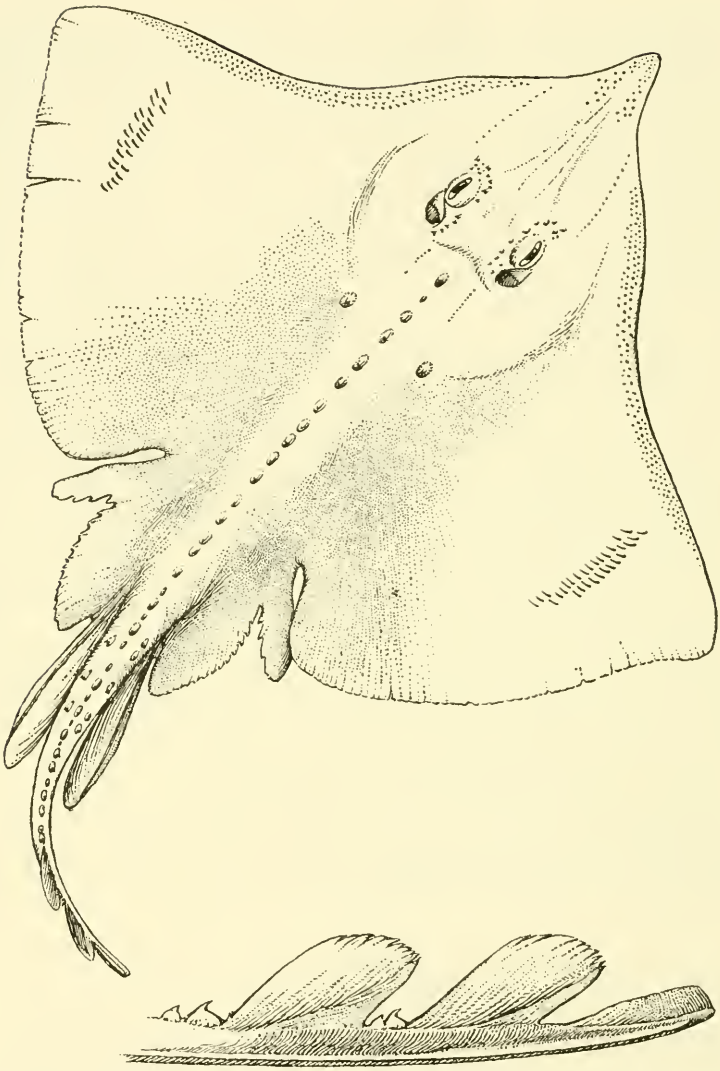

Figure 5. *Raja garricki*, dorsal view of type, mature male 975 mm long; end of tail showing dorsal fins and caudal fin, about x 0.5.

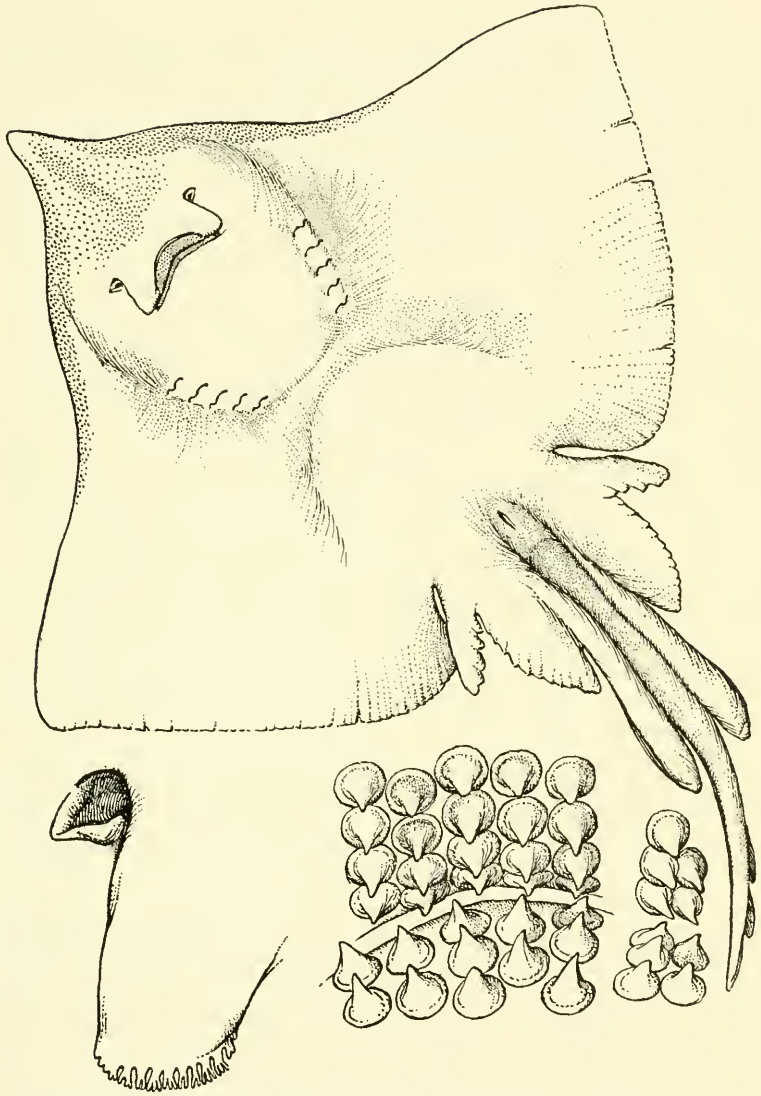

Figure 6. *Raja garricki,* ventral view of specimen shown in Figure 5; right hand nostril and nasal curtain, about x 1; upper and lower teeth from center and from near outer part of jaws, about x 2.4.

*Distinctive Characters.* Characters in combination which distinguish *garricki* from other species of the genus *Raja* are: margins of disc anterior to outer angles of pectorals sinuous (at least in the males, the female has not been seen); snout pointed (Fig. 5); disc with a single row of large thorns along the midbelt extending from the nuchal region to the first dorsal fin, with an interrupted row on either side on the tail; a single large scapular thorn on each side of the midrow; lower surface with dark mucous pores anterior to the abdominal region (Fig. 7).

*Comparison with previously known species.* The only western Atlantic skates with a disc somewhat the shape of *garricki* and with dark pores on the under surface are *laevis*, *oregoni*, *flavirostris*, *platana* Günther 1880 and *agassizi* Müller and Henle 1841. But *garricki* differs from all of these (excepting some specimens of *agassizi*) by having a continuous row of thorns along the mid-line of disc and tail, extending from the nuchal region to the dorsals whereas the midrow of thorns on the above mentioned species does not extend much, if any, forward beyond the axils of the pectorals. And *garricki* may be distinguished from *agassizi* by the position of its first dorsal which originates much nearer to tip of tail than to tips of pelvics (nearer pelvics than tip of tail on *agassizi*) and by a dorsal fin interspace much shorter than base of either first or second dorsal. Also, the dark pores on the under surface of *garricki* are much more conspicuous and more numerous than on *agassizi*.

In the eastern Atlantic, including southern Africa, only *batis* and *oxyrhynchus* have a narrow snout together with dark pores below, and both of these lack the thorns along the midline of the disc that are present on *garricki*.

*Garricki* falls with *rhina* and *flavirostris* of the eastern Pacific in general shape of disc and in the presence of dark pores below. But *garricki* differs in spination from *rhina* by having scapular thorns and a single row of midline thorns on the disc but no additional small thorns in the midzone. *Flavirostris* has one nuchal thorn but no other midline thorns on disc.

*Garricki* somewhat resembles *lempricri* Richardson 1844-48, *porosa* Günther 1874, and *australis* Macleay 1884 in the Indo-Australian region in having a narrow snout and dark pores

(Munro 1956, p. 15) on the lower surface but its row of thorns along the midzone of disc sets it apart from these species which lack thorns in this area and from *gudgeri* Whitley 1940 which has but a very short row along the middle of the back as well as a very long and narrow snout resembling that of *oxyrhynchus*. *Garricki* closely resembles *macracauda* Ishiyama 1955 from Japan in shape of disc and in having dark pores below but, except for 2 nuchals, *macracauda* lacks thorns along the midline of disc and has no scapular thorns.

*Description of holotype.* Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 78.3; length 59.0.

Snout length. — In front of orbits 18.3; in front of mouth 19.0.

Orbits. — Horizontal diameter 3.5; distance between 5.4.

Spiracles. — Length 3.1; distance between 6.9.

Mouth. — Breadth 8.5.

Exposed nostrils. — Distance between inner ends 9.1.

Gill openings — Length, 1st 1.5; 3rd 1.8; 5th 1.5; distance between inner ends, 1st 15.7; 5th 9.4.

First dorsal fin. — Vertical height 2.8; length of base 4.0.

Second dorsal fin. — Vertical height 2.6; length of base 3.7.

Pelvics. — Anterior margin 10.6.

Distance. — From tip of snout to center of cloaca 55.4; from center of cloaca to 1st dorsal 30.7, to tip of tail 44.6; from rear end of 2nd dorsal base to tip of tail 5.0.

Interspace between. — 1st and 2nd dorsals 1.2.

Disc about 1.3 times as broad as long, maximum angle in front of spiracles about 78°; anterior margins weakly concave just posterior to tip of snout, thence slightly convex followed by a stronger concavity culminating about midway between tip of snout and outer corners which are sharply rounded; posterior margins at first about straight from outer corner, then gently rounded, as is inner margin. Axis of greatest breadth about 62 per cent of distance back from tip of snout toward axils of pectorals. Tail with a narrow lateral fold, low down on each side, beginning abruptly in advance of tips of pelvics by a distance equal to about three-fourths the interorbital width and continuing almost to extreme tip of tail, widest opposite dorsals

and caudal membrane; length of tail from center of cloaca to origin of first dorsal fin 0.56 times as great, and to its tip 0.80 times as great, as distance from center of cloaca to tip of snout.

A patch of 11 small thorns immediately in front of left orbit and 7 in front of right followed by a row of 7 or 8 larger thorns along inner margins of orbits ending slightly posterior to rear margins of spiracles. End of snout densely covered with small thorns and prickles extending rearward over rostral process in diminishing numbers; a band of small thorns and prickles extends along edge of disc from tip of snout to about opposite foremost alar thorns, narrow near end of snout, then widening and the prickles coarsening half way from snout to opposite orbits, again smaller rearward. A single stout thorn on each side of median row in scapular region; a median row of prominent thorns from nuchal region to first dorsal fin, of which 4 are in the nuchal-scapular area, the second of these being very small, followed by 32 thorns of which 7 are anterior to pectoral axil and 25 on tail, these latter somewhat closer together and more uneven in size; a row of 3 large thorns aside the median row on left side of the mid-tail region and 5 on the right side, unevenly spaced; 2 prominent thorns between dorsal fins. All the thorns on body and tail that have retained their sharp points are directed obliquely rearward. Alar thorns prominent, in two to three irregular rows, 26 on left side of disc, 30 on right; rest of body, pelvics and tail smooth as is space between orbits and skin over eyes; first and second dorsals with a few scattered prickles.

A short longitudinal row of 11 dark pigmented mucous pores on the right side of first nuchal thorn and of 8 on the left side, at a distance from the midline about two-thirds as great as diameter of orbit. The presence of mucous pores, in a conspicuous pattern in this region, has thus far been found only on *Raja fyllae* Lütken 1887, *laevis* and in the new species *oregoni* and *clarkii* among skates known from the western North Atlantic. (See Bigelow and Schroeder, 1954, p. 57.)

Lower surface with prickles in front of and aside the mouth, most dense toward end of snout and along margins of disc where they extend rearward about three-fifths the distance toward outer

angle of pectoral; a few exceedingly small widely scattered prickles over parts of the scapular and abdominal regions and on pelvics; rest of lower surface naked.

Snout in front of orbits 5.2 times as long as orbit, its length in front of mouth 2.1 times as great as distance between exposed nostrils. Distance between orbits about 1.6 as great as length of orbit. Orbit 1.1 as long as spiracle. Nasal curtain fringed; expanded posterior (outer) margins of nostrils smooth, without fringes. Upper and lower jaws strongly arched centrally. Teeth $\frac{35}{35}$ more nearly in quincunx arrangement than in longitudinal rows, with circular or ovate base, those in upper jaw in median sector of mouth with a prominent upright cusp, the adjacent teeth with cusps pointing toward corner of mouth, those near corners of mouth with flattened crowns; lower teeth similar but median teeth with cusps at slight angle, which increases outwardly.

Distance between first gill openings 1.7 times as great as between exposed nostrils; between fifth openings 1.0 times; first gill openings 1.1 times as long as fifth and about 0.2 as long as breadth of mouth. First and second dorsals similar in size and shape. Interspace between dorsals 0.33 as long as base of first dorsal. Caudal membrane base equal to that of first dorsal. Pelvics deeply concave, strongly scalloped along anterior side of excavation, moderately so rearward; anterior margin 0.58 as long as distance from its own origin to rear tip of pelvic; anterior lobe slender, including four radial cartilages beside the first stout one; posterior lobe moderately convex, with a narrowly rounded tip, extending about one-half the distance from axil of pectorals toward first dorsal. Claspers reaching beyond tips of pelvics by a distance equal to seven-tenths the distance from front of orbits toward tip of snout.

Rostral cartilage firm, extending nearly to tip of snout. Anterior pectoral rays reaching about three-sevenths the distance from front of orbits toward tip of snout.

*Color.* Upper surface plain brownish without spots or other markings. Lower surface pale bluish dusky on disc, pelvics and claspers, tail tending more to pale brownish. Scattered black

pores anterior to abdominal region, most numerous around mouth and in front of level of mouth to near tip of snout. (Fig. 7.)

The other known specimen of this species, a male 1019 mm long, differs as follows: maximum angle of disc in front of spiracles 74°, axis of greatest breadth about 67 percent of distance back from tip of snout toward axils of pectorals; length of tail from center of cloaca to origin of first dorsal fin is 0.53 times as great and to its tip 0.78 times as great as from center of cloaca to tip of snout. There is a patch of 8 small thorns along anterior edge of each orbit; fewer prickles over rostral process which is

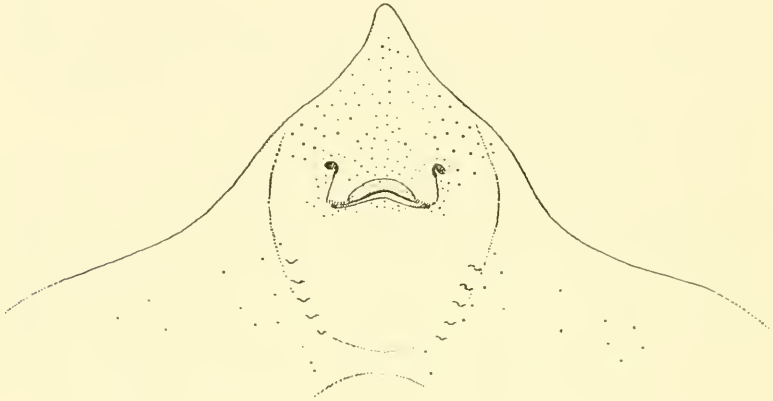

Figure 7. *Raja garricki,* ventral view of head to show dark mucous pores, about x 0.1.

naked toward orbits; 5 thorns in the mid row in the nuchal-scapular area, followed by 41 thorns to first dorsal, of which 8 are anterior to pectoral axils and 33 are on tail; a row of 5 unevenly spaced large thorns on left side of tail aside the median row, 2 on right; 31 alar thorns on left and 33 on right side of disc. The mucous pores in nuchal region are in a series of 9 on each side. On the lower surface the prickles along the anterior margin of disc extend less than halfway toward outer angle of pectoral.

Known only from the offing of Cape San Blas, Florida, in 260 fathoms. Named for Dr. J. A. F. Garrick of Victoria University College, Wellington, in recognition of his work on elasmobranchs of New Zealand.

### Raja clarkii sp. nov.

Figures 8, 9

*Study Material.* Immature male, 665 mm in total length, holotype, U. S. Nat. Mus. No. 156712, another male 580 mm long, and a female 747 mm long, paratypes, M. C. Z. No. 39618, all from the northern part of the Gulf of Mexico, Lat. 28°32′N, Long. 86°20′W, in 260 fathoms, "Oregon" station 1277.

*Diagnostic Features.* The presence of 1 to 3 pairs of prominent white roundish or barlike markings on the upper surface of disc in combination with a broad snout and a band of formidable and very sharp thorns which extend along the lower surface from the tip of snout almost to the extreme outer margin of pectorals sets off *clarkii* from all other known members of the Rajidae.

*Description of holotype.* Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 68.7; length 55.0.

Snout length. — In front of orbits 14.2; in front of mouth 15.3.

Orbits. — Horizontal diameter 3.2; distance between 3.6.

Spiracles. — Length 3.3; distance between 6.0.

Mouth. — Breadth 8.7.

Exposed nostrils. — Distance between inner ends 4.5.

Gill openings. — Length, 1st 1.2; 3rd 1.6; 5th 1.3; distance between inner ends, 1st 14.9; 5th 8.9.

First dorsal fin. — Vertical height 1.7; length of base 4.3.

Second dorsal fin. — Vertical height 1.7; length of base 4.3.

Pelvics. — Anterior margin 11.7.

Distance. — From tip of snout to center of cloaca 53.4; from center of cloaca to 1st dorsal 34.6; to tip of tail 46.6; from rear end of 2nd dorsal to tip of tail 3.2.

Interspace between. — 1st and 2nd dorsals 0.6.

Disc about 1.25 times as broad as long; outline of snout as in Figure 8; anterior margin rather strongly convex in front of orbits, thence concave with outer corners broadly rounded; pos-

terior and inner margins gently rounded. Axis of greatest breadth about 70 per cent of distance back from tip of snout

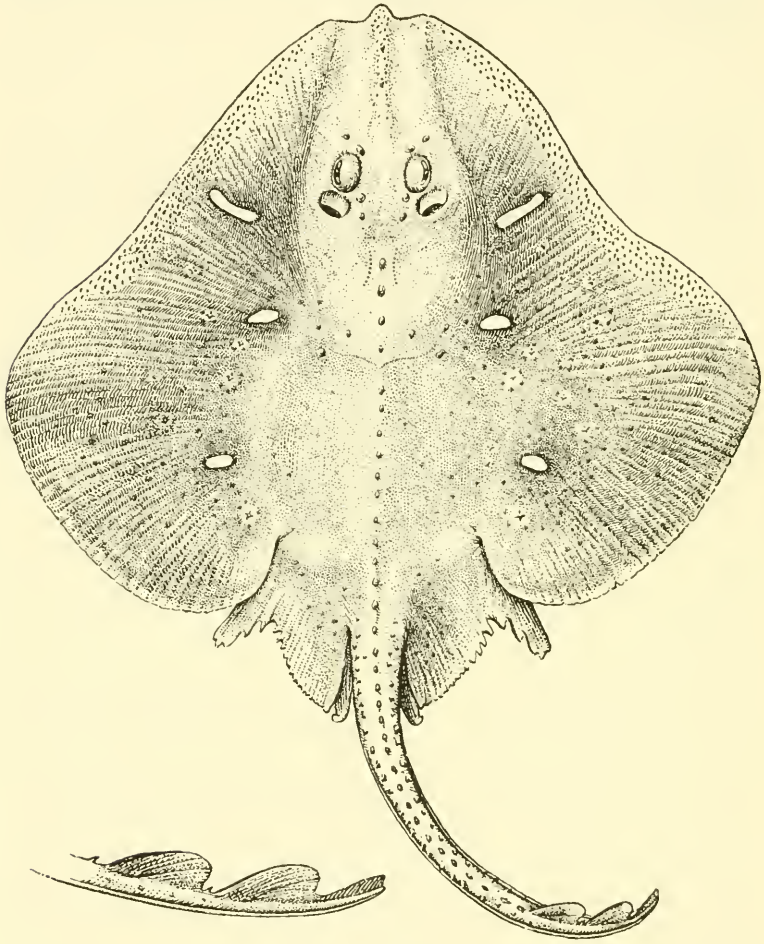

Figure 8. *Raja clarkii*, dorsal view of type, immature male 665 mm long; end of tail showing dorsal fins and caudal fin, about x 0.5.

to axils of pectorals. Tail with a narrow lateral fold, low down on each side, beginning just beyond tips of pelvics and continu-

ing almost to extreme tip of tail, widening posteriorly, widest opposite dorsals; length of tail from center of cloaca to origin of

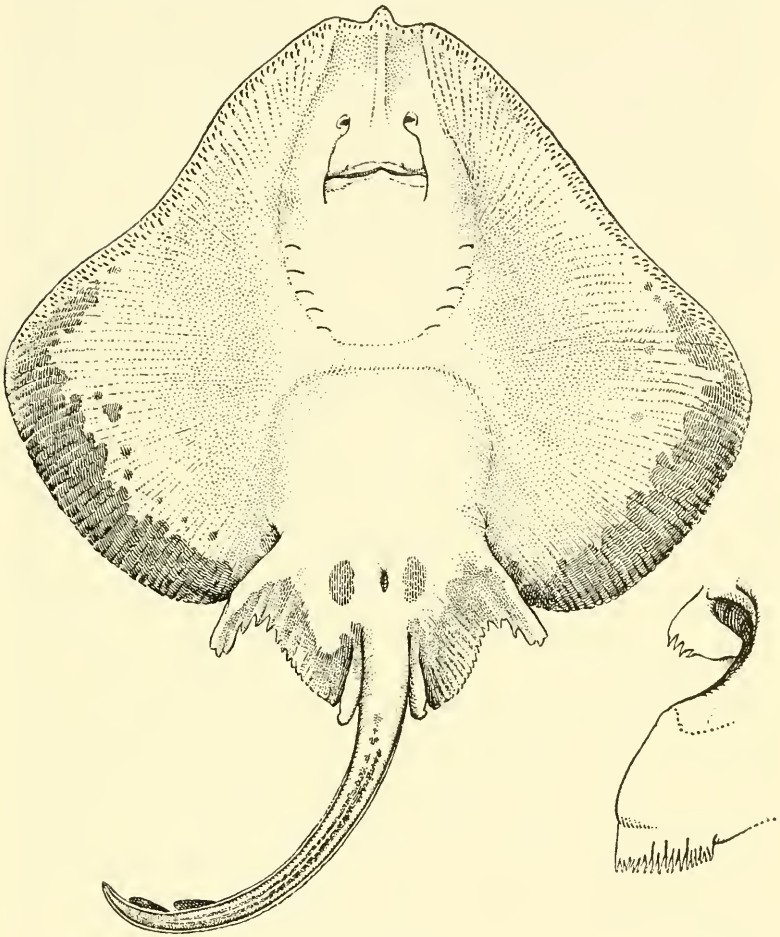

Figure 9. *Raja clarkii,* ventral view of specimen shown in Figure 8; right-hand nostril and nasal curtain, about x 1.1.

first dorsal fin 0.65 times as great and to its tip 0.87 times as great as distance from center of cloaca to tip of snout.

A small thorn in advance of each orbit by a distance of about ⅓ orbit's diameter; a larger thorn immediately next to inner anterior edge of orbit, with one at posterior end of orbit and another smaller one inward toward median line, this last opposite rear end of spiracle. Snout and disc in front of orbits and space between orbits with small thorns, many with stellate bases, and with prickles; two stouter thorns over rostral process, located 27 and 47 per cent, respectively, in the distance from tip of snout toward orbits; a band of small thorns extends along edge of disc from near tip of snout to about opposite scapular region. A triangular patch of three thorns on each side of median row in scapular region; a median row of 34 thorns from nuchal region to first dorsal, of which 4 are in the nuchal-scapular area, followed by 7 anterior to pectoral axils and by 23 on tail, all of these of about equal size and equally spaced; a row of thorns on each side of the median row beginning about opposite axils of pelvics and continuing to opposite first dorsal, many with sharp hooked points directed rearward; 1 thorn between dorsals. Alar thorns not yet exposed; rest of disc with scattered prickles, very sparse in some areas and mostly minute; also small thorns and prickles on tail in addition to the three prominent rows, mostly low down, from near axils of pelvics nearly to tip of tail; pelvics smooth; dorsals with an occasional prickle. A longitudinal row of 12 dark ringed mucous pores on right side and 13 on left outward from first nuchal thorn by a distance about one-third the diameter of orbit.

Lower surface with prickles along rostral process out to tip of snout with a few scattered over translucent area in front of nostrils; also a band of strong, very sharp thorns all of about the same size, curving inward or obliquely rearward, extending from near end of snout almost to outer angle of pectoral, in a band about 0.4 times as wide as distance between orbits, these characters in combination being a striking feature of this species; rest of lower surface smooth.

Snout in front of orbits 4.4 times as long as orbit, its length in front of mouth 3.4 times as great as distance between exposed nostrils. Distance between orbits about 1.1 as great as length of orbit. Orbit about the same length as spiracle. Nasal curtain fringed; expanded posterior (outer) margins of nostrils with a

few fringes. Upper and lower jaws moderately arched. Teeth $\frac{63}{61}$, in part in longitudinal rows and in part more or less in quincunx, with rounded base and triangular cusp, inclined toward corners of mouth.

Distance between first gill openings 3.3 times as great as distance between exposed nostrils; between fifth openings 2.0 times; first gill openings about as long as fifth and about 0.14 as long as breadth of mouth. First and second dorsals similar in size and shape. Interspace between dorsals 0.14 as long as base of first dorsal. Caudal membrane with base a little shorter than that of first dorsal base. Pelvics deeply concave, strongly scalloped along anterior side of excavation, moderately so rearward; anterior margin 0.78 as long as distance from its own origin to rear tip of pelvic; anterior lobe slender, including four radial cartilages besides the first stout one; posterior lobe moderately convex, with a narrowly rounded tip, extending a little less than half the distance from axils of pectorals toward first dorsal. Claspers reaching beyond tips of pelvics by a distance equal to less than half diameter of orbit.

Rostral cartilage firm, extending nearly to tip of snout. Anterior pectoral rays reaching anterior edge of disc but falling short of end of rostral cartilage which continues into snout protuberance.

*Color.* Upper surface pale brown with darker punctulations scattered over disc, pelvics and more or less of tail. Three pairs of prominent white markings on disc, of which one pair is opposite spiracles, bar-like, somewhat curved, and a little longer than interorbital space; a second pair about half as long and opposite scapular region and a little closer together than first pair; a third pair about size of second pair, in line with first pair and opposite eighth thorn from nape in median series. Lower surface white with a wide irregular grayish band along posterior and inner margins, extending from a little in advance of outer angles to axils of pectorals and along rear margin of pelvics; also a pair of grayish spots opposite cloaca and a few small ones here and there on disc, with some gray markings on tail and on claspers.

The other two known specimens of this species, a male 580 mm long and a female of 747 mm agree very closely with the holotype

in proportional dimensions and in the formidable band of sharp thorns on the under surface along the anterior margin of the disc. The chief differences are as follows. They have a disc 1.2 times as wide as long, and 65.3 and 65.0 per cent, respectively, of the total length of the specimens, as compared with 1.25 times as wide and 68.7 per cent as long as the holotype, while the length of tail from center of cloaca to origin of dorsal fin is 0.69 times as great and to its tip 0.90 times as great as distance from center of cloaca to tip of snout on both specimens as compared with 0.65 and 0.87 times, respectively, on the holotype. The two thorns over the rostral process on the 580 mm male are located 34 and 58 per cent in the distance from tip of snout to orbits while the 747 mm female has three such thorns located 23, 44, and 60 per cent in this distance. There are 40 thorns in the median row on the 580 mm male of which 28 are posterior to the pectoral axil, and there are 38 thorns on the 747 mm female of which 27 are posterior. The mucous pores number 9 on one side and 11 on the other on the smallest skate and 14 on each side of the largest which also has more numerous prickles on lower surface over the translucent area in front of nostrils than on the other two specimens. The tooth count of the 580 mm male is $\frac{61}{59}$, and of the 747 mm female $\frac{60}{60}$.

The upper surface of the female has the three pairs of prominent white markings of about the same relative size and location as on the holotype but below there are no gray spots in the cloacal region while there is an oval gray spot on each side of the rostral process near its tip. The small male has only one pair of white spots above, opposite the spiracles, roundish, and about half the size of the orbit.

Known only from the northern part of the Gulf of Mexico, Lat. 28°32′N, Long. 86°20′W, in 260 fathoms. Named for Robert S. Clark in recognition of his revision of European skates and rays.

### Crurirаja rugosa sp. nov.

Figures 10, 11

*Study Material.* Immature male, 367 mm in total length, holotype, U. S. Nat. Mus. No. 156713 from the northeastern part of the

Gulf of Mexico, in 200-300 fathoms, trawled by the "Oregon," station number not known.

*Distinctive Characters.* *Cruriraja rugosa* differs from all other known members of its genus in that the under side of its tail is covered with minute prickles, this area being smooth in all other species.

*Comparison with previously known species.* From other western Atlantic species it differs as follows: from *atlantis* Bigelow and Schroeder 1948, by the short space between its dorsals, equal to about one-fourth the length of first dorsal base (about 2½ times the dorsal base on *atlantis*); from *poeyi* Bigelow and Schroeder 1948, by its prickles on disc, the presence of two nuchal thorns and of a single row of thorns on the midline of tail (disc without prickles, no nuchal thorns, midline row of thorns on tail divides into two rows posteriorly on *poeyi*). It differs from the two species of *Cruriraja* known from South Africa, as follows: from *parmomaculata* (von Bonde and Swart 1924, p. 9, pl. 21, fig. 2) in having a wide space lacking thorns along the midline of disc between the 2 nuchal thorns and axils of pectorals, by lacking scapular thorns, and by its plain coloration (*parmomaculata,* described from a young specimen 181 mm in total length, has a continuous row of thorns from the nuchal region to the first dorsal, 1 scapular thorn on each side and 14-18 blackish brown spots of varying size on the disc). *Rugosa* with its widely interrupted row of thorns along the midline of back, its lack of thorns in the scapular region and the rounded rear margins of its dorsal fins may be readily distinguished from *durbanensis* (von Bonde and Swart 1924, p. 11, pl. 22, fig. 1) which has an uninterrupted row of thorns along the midline of back from nape of first dorsal on a male 232 mm long, 2 scapular thorns on each shoulder and dorsal fins which are pointed posteriorly; and on a female 311 mm long the midrow of thorns ends about halfway along tail, leaving a wide thornless space before first dorsal.

*Description of holotype.* Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 59.4; length 46.0.

Snout length. — In front of orbits 12.0; in front of mouth 15.0.

Orbits. — Horizontal diameter 4.5; distance between 2.8.

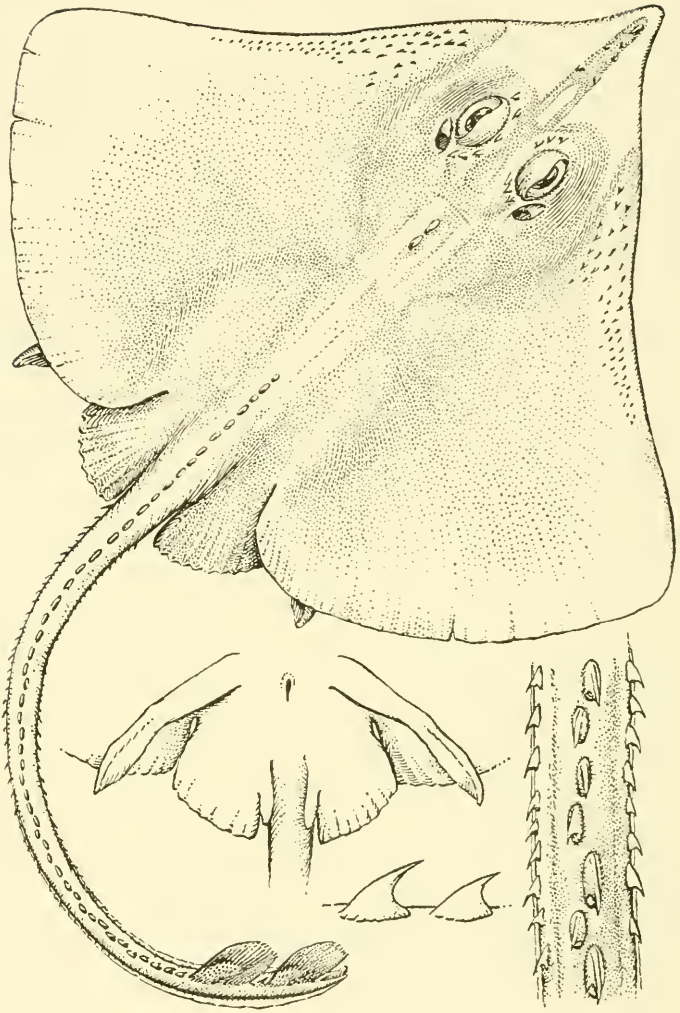

Figure 10. *Cruriraja rugosa,* type, immature male 367 mm long; pelvic fins about x 0.5; section of tail about x 2; first 2 thorns in front of dorsal fin about x 3.

Spiracles. — Length 2.2; distance between 6.5.

Mouth. — Breadth 6.3.

Exposed nostrils. — Distance between inner ends 5.5.

Gill openings. — Length, 1st 1.5; 3rd 1.5; 5th 1.2.

First dorsal fin. — Vertical height 2.7; length of base 4.5.

Second dorsal fin. — Vertical height 2.6; length of base 3.3.

Pelvics. — Length of limb 15.0.

Distance. — From tip of snout to center of cloaca 40.6; from center of cloaca to 1st dorsal 48.0; to tip of tail 59.4; from rear end of 2nd dorsal base to tip of tail 2.5.

Interspace between. — 1st and 2nd dorsals 1.1.

Disc about 1.3 times as broad as long, maximum angle in front of spiracles about 87°; anterior margins from snout to outer corners of pectorals slightly sinuous, the corners abruptly rounded; posterior and inner margins gently rounded. Axis of greatest breadth about 70 per cent of distance back from tip of snout to axils of pectorals. Tail with a lateral fold, low down on each side beginning about 55 per cent of the distance from straight. Teeth $\frac{43}{42}$, arranged in quincunx, with ovate base and axils of pelvics toward tip of tail, very narrow anteriorly but widening considerably on approaching tip of tail; length of tail from center of cloaca to origin of first dorsal 1.2 times as great and to its tip 1.45 times as great as distance from center of cloaca to tip of snout.

Inner margin of left orbit with 6 thorns, 2 of which are anterior, 1 midway and 3 posterior; right orbit with 3 anterior and 3 posterior thorns, the last two in each case being opposite the spiracles. A staggered row of 4 thorns on anterior part of rostral process followed by a pair of rostral thorns a little more than half the distance from tip of snout toward a line connecting anterior margins of orbits; a band of sharp, backward pointing thorns along margins of disc, beginning opposite anterior edge of orbits and ending about opposite scapular region, the thorns decreasing in size and the band narrowing posteriorly. Two prominent nuchal thorns followed by a naked area and then by a midrow of 47 thorns beginning about 1½ eye's diameter in advance of axils of pectorals and continuing uninterrupted to first dorsal fin, becoming staggered posteriorly, but in a single row; an additional row of smaller thorns each side of the midrow,

low down on tail, beginning about opposite tips of pelvics and extending nearly to first dorsal where it merges with a band of prickles; all the tail thorns pointing strongly rearward; a single thorn between dorsals. Upper surface of disc (including skin over eyes) covered with minute prickles except along posterior margins and on extreme tip of snout; pelvics naked; tail prickly, everywhere except along the midzone; dorsals densely prickly. Lower surface of disc entirely smooth, but tail covered with minute prickles from about opposite tips of pelvics to opposite origin of second dorsal.

Snout in front of orbits 2.8 times as long as orbit, its length in front of mouth about 2.7 times as great as distance between exposed nostrils. Distance between orbits 0.65 times as great as

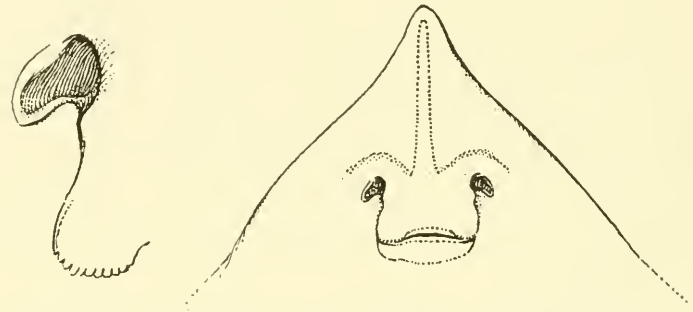

Figure 11. *Cruriraja rugosa,* ventral view of head, about x 0.5; right-hand nostril and nasal curtain, about x 2.

length of orbit. Orbit twice as long as spiracle. Nasal curtain with a very short, blunt fringe, expanded outer margins of nostrils smooth, without fringes. Upper and lower jaws nearly short triangular cusp.

Distance between first gill openings twice as great as distance between exposed nostrils; between fifth openings about 1.2 times; first to fourth gill openings about 1.3 times as long as fifth and about 0.25 as long as breadth of mouth. First and second dorsals similar in shape the first slightly the larger. Interspace between dorsals 0.25 times as long as base of first dorsal. Caudal fin very small. Anterior division of pelvics long and slender reaching

beyond tips of posterior lobe when pulled back; posterior lobe with 12 rays, quadrate, the rear margin gently rounded and faintly scalloped, the tips reaching but little beyond rear margin of disc. Claspers failing to reach tips of pelvics by a distance equal to half the diameter of eye.

Rostral cartilage firm, narrow, extending nearly to tip of snout. Anterior pectoral rays reaching 22 per cent the distance from front of orbits toward tip of snout.

*Color.* Upper surface of disc brownish with a bluish tinge, without spots or other markings; tail pale brownish; dorsal brownish with a pale area basally. Below pale bluish on disc, the tail pale brown.

Known only from a single specimen, an immature male 367 mm long, trawled in 200-300 fathoms in the northeastern part of the Gulf of Mexico.

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**Bulletin of the Museum of Comparative Zoology**

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# THE GENERAL HISTOLOGY AND TOPOGRAPHIC MICROANATOMY OF *AUSTRALORBIS GLABRATUS*

By CHIA-TUNG PAN

The Department of Tropical Public Health, Harvard School of Public Health, Boston, Massachusetts

WITH EIGHTEEN PLATES

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

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No. 3 — *The General Histology and Topographic Microanatomy of Australorbis glabratus*[1]

By Chia-Tung Pan[2]

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## INTRODUCTION

In a series of investigations on the potentialities of biological control of schistosomiasis, our efforts thus far have been concentrated on the accumulation of fundamental biological data on the snail vector, *Australorbis glabratus*. It was early realized that a knowledge of the normal histology of this snail was essential in order to permit a recognition of specific pathological alterations which might be induced by microorganisms. The present study was undertaken to satisfy this objective.

The gross anatomy of *A. glabratus* has been described by Baker (1945), and Paraense and Deslandes (1955). However, information on the histology of this snail is sparse (Faust and

Hoffman, 1934; von Brand and Files, 1947; Marcuzzi, 1950; Paraense and Deslandes, 1955) and inadequate as a basis for studying pathological changes. Despite the fact that the parasitic trematodes of man are known to utilize at least one fresh-water molluscan intermediate host, we have not discovered a comprehensive study of the histology of a single important molluscan host. The paucity of knowledge of the normal histology of fresh-water snails has been recognized recently by workers in this field, and some papers dealing with the digestive and genital tracts of a few fresh-water snails (Holm, 1946; Carriker and Bilstad, 1946; Abdel-Malek, 1954 a, b) have appeared.

The excellent monograph by Baecker (1932) on the micromorphology of *Helix* and other pulmonates, proved to be exceptionally helpful in the present studies.

## MATERIAL AND METHODS

Laboratory-raised *Australorbis glabratus* of Puerto Rican origin were used. Our colony was started from stocks sent by Dr. Redginal I. Hewitt of the Lederle Laboratories, New York, and Dr. Donald V. Moore then at New York University. Although snails of various sizes were used, the descriptions given here are based mainly on specimens measuring between 9 and 20 mm. in size.

Snails were removed from the shell by crushing gently between two glass slides. The shell fragments were then separated with fine forceps under a dissecting microscope. With practice, intact snails could usually be obtained readily in this manner. The shell-free snails were immediately fixed either in a coiled or stretched position. A small amount of fixative was injected into the mantle cavity, employing a 27-gauge needle attached to a tuberculin syringe to insure rapid fixation of internal organs. Air in the mantle cavity was always removed by gentle manipulation under a dissecting microscope.

Zenker's or Maximow's fixative gave the best results for cytological study but hardened the genital tract and certain genital organs considerably. Formic acid Bouin's or Bouin's mixture had less tendency to harden the tissue, but the cytological structures were less well preserved. A solution of 5 per cent formic

acid in Zenker's stock was tried with results equal to those with Zenker's. Carnoy's and Newcomer's mixtures and 10 per cent neutral formalin were used for special purposes. Fixation was considered complete after 4 to 48 hours with aqueous mixtures, and after 3 to 6 hours with alcoholic solutions. Tissues were imbedded in paraffin (M. P. 56° C — 58° C) at 60° C and sectioned between 6 and 13 microns. Since it was necessary to remove all of the sand grains in the digestive tract for complete serial sections, the method of Carriker and Bilstad (1946) was used to obtain sand-free snails.

Lillie-Mayer's, Delafield's, Mallory's and Heidenhain's hematoxylins were used for nuclear staining, and eosin Y or phloxine B were employed as counter stains. Maximow's hematoxylin-azure II-eosin in thin sections gave excellent results for cytological studies. Special staining techniques used for the identification of various tissue components or structures were: Mallory's and Gomori's trichrome stains for connective tissue elements; Wolbach's Giemsa stain variant; Feulgen reaction for deoxyribonucleic acid; aldehyde fuchsin and acid orcein for elastic tissue; Hotchkiss' (1948) periodic acid-Schiff (PAS) for carbohydrate; thionin (at pH 4.0 to 5.0) and toluidine blue 0 for metachromatic substance; Bielshowski-Glees' and Bodian's silver impregnation; Korson's technique (1951) for nucleic acids; alcian blue 8GS (Steedman, 1950) for acid mucopolysaccharides; and Millon's reaction (Pearse, 1953; Lillie, 1954).

In the course of this histological study, two types of microorganisms — an acid-fast bacillus and a yeast-like organism — were encountered. Both organisms were always found associated with histopathologic changes (Pan, 1956). Since these histopathologic changes frequently aided in identifying the normal histologic structures of *A. glabratus*, reference will be made to the above-mentioned two microorganisms in the later sections.

The terminology used to designate various organs is based on Baker's monograph (Baker, 1945) on planorbid snails. The measurements of snails are given in shell diameter and thickness.

## DESCRIPTION
## TOPOGRAPHIC MICROANATOMY

Since a knowledge of the topography of various organ systems is necessary for the description of the histology of *Australorbis glabratus,* a brief account of its topographic microanatomy is given. One longitudinal and four cross-sections were selected to show the relations of various organs. Although the sections were selected on an arbitrary basis, it is believed they provide an adequate perspective of the microanatomy of the organ systems. The photomicrographs of these sections are self-explanatory, and, therefore, only important landmarks are indicated.

Figure 1 is an approximate median longitudinal section of a stretched snail measuring 15.0 x 5.1 mm. Figures 2 to 5 were taken under higher magnification and represent four areas of Figure 1. Figure 6 is a cross-section through the ganglion ring, and Figure 7 is through the spermatheca; these were from the same snail which measured 12.8 x 4.0 mm. Figure 8 is a cross-section through the stomach of a snail (10.7 x 4.1 mm.), and Figure 9 is through the overlapping area of the liver and ovotestis of a snail measuring 20.0 x 6.5 mm.

The important landmarks which should be noted in Figures 1 to 9 are to be found in the appropriate captions.

## HISTOLOGY

Baecker (1932) divided the various systems of land pulmonates into two major categories, tissue (*Gewebe*) and organ (*Organe*), and made several subdivisions for each category. This classification is logical but has considerable overlapping. The following classification of the various tissues and organ systems of *Australorbis glabratus* was adopted in the present study:

I. Epithelium
II. Connective Tissue
III. Muscular Tissue
IV. Nervous System and Sensory Organs
V. Circulatory System
VI. Respiratory System
VII. Renal Organ
VIII. Alimentary System
IX. Reproductive System

## I. Epithelium

Anatomically the epidermal tissue can be divided into three major zones: (a) that exposed to the outer world, including the head-foot organ and the mantle collar, (b) that always protected by the shell, including the mantle, columellar muscle, liver and ovotestis, and (c) the mantle cavity surface (respiratory surface). Baecker (1932) demonstrated that the epidermal tissue in land pulmonates consists only of a simple epithelium over the body surface. This is also the case in *A. glabratus* except in one small area at the dorsal rim of the mantle collar where there is pseudostratified columnar epithelium (Figs. 1 e, 11). The epidermal sheet rests on a basement membrane which is supported by a layer of connective tissue containing various amounts of smooth muscle fibers. The coelomic cavity is lined incompletely with flat cells.

*Epithelium covering the exposed body surface.* The surface of the foot or the sole is covered with a layer of tall columnar epithelial cells (*ca.* 22.5 microns in 18.8 x 6.5 mm. snail) possessing oval to elongated vesicular nuclei, relatively rich in chromatin. The free surface of these cells is heavily invested with long cilia. A row of basal bodies, each of which is connected with a cilium, lies immediately beneath the plasma membrane. The basement membrane can be seen clearly in sections cut at right angles and stained with Gomori's, Mallory's trichrome, or PAS. The epidermal cells on the foot surface appear to rest on the basement membrane with their short processes embedded therein. The cytoplasm of these cells is granular and lightly basophilic. The nucleus is located between the middle and basal third of each cell (Fig. 10). The cilia become sparse and disappear over the side wall of the head-foot organ where the tall, columnar, simple epithelium of the foot surface is replaced by low columnar-to-cuboidal simple epithelium. The epidermal cells of the mantle collar are also of this type except in a small area at the dorsal rim where there is pseudostratified columnar epithelium (Fig. 11). The cytoplasm of these cells is granular, moderately basophilic, and contains yellowish-brown pigment. This pseudostratified epithelium has a glandular appearance like that of the prointestine and may prove to have functions connected with shell regeneration.

*Epithelium covering the area usually protected by the shell.* This area includes the mantle surface, most of the columellar muscle, the liver and ovotestis (Fig. 1). The epithelial cells are characterized by having a dense deposit of brownish-black pigment in the cytoplasm, which usually obscures cellular structures. This pigment, named melain by Simroth in 1903 (Baecker, 1932), is not seen in the other two zones. Since this pigment stains green with Giemsa or thionin and reduces ammine silver, it is probably related to melanin of higher animals. The epithelial cells covering the mantle are low columnar to cuboidal with parabasal, round nuclei (Fig. 12). These cells are transformed into flat or squamous epithelial cells in the region of the liver, ovotestis and columellar muscle. The basement membrane and supporting connective tissues are delicate. The nuclei of these cells contain fewer chromatin granules than do those of cells covering the head-foot area.

*Epithelium covering the mantle cavity.* Three types of epithelium can be recognized in the mantle cavity. These are flat cells, cuboidal cells without cilia, and columnar cells which may be ciliated. The flat cells cover the surface of the wall of the coelomic cavity. The rest of the mantle cavity surface, except the surface of the three ridges (rectal, dorsal and kidney ridges), is covered with a sheet of cuboidal epithelial cells with round, parabasal nuclei (Fig. 13). The rectal, dorsal and kidney ridges are covered with a sheet of columnar cells that are very tall at the summits of the ridges and are provided with dense cilia in this area. These tall cells measure 30 microns in height in a snail of 12.8 x 4.0 mm. Unlike those of the foot surface, they rest on the basement membrane without anchoring short processes. The nuclei are oval, rich in chromatin and located in the middle third of the cytoplasm. The granular cytoplasm has three zones, the surface and the basal zones staining acidophilic, and the middle zone basophilic. Cilia arise from basal bodies located beneath the plasma membrane. The nuclei of the cuboidal cells are spherical and located near the basement membrane. The granular cytoplasm of the flat and of the cuboidal cells stains lightly basophilic throughout and these cells lack cilia. These two types of cells also have a smooth basal surface where

it is in contact with the basement membrane. Mucus-secreting cells (goblet cells) are scattered among the columnar and cuboidal cells and secrete mucus through the interstices between epithelial cells. Pigment does not occur in the epithelial cells in the mantle cavity.

## II. Connective Tissue

The connective tissue of *A. glabratus* occupies the region between the organs and tissues and forms a membranous covering or sack enclosing the organs in the body cavity. The connective tissue contains various cellular and fibrous components and may be classified as to type depending on the relative proportion of the individual components. Baecker (1932) recognized four cellular components (*Fibroblasten, Blasenzellen, Körnchenzellen,* and *Pigmentzellen*) and two fibrillar components (*praekollagene Fibrillen* and *Gitterfasern*) in the connective tissue proper of land pulmonates. In *A. glabratus* the cellular components consist of: (a) fibroblasts, (b) pigment cells, (c) vesicular cells, and (d) mucous cells, and the fibrous components consist of collagenous-like fibers and delicate fibrils on the muscle fibers (*Gitterfasern* of Baecker).

Two distinctly different types of connective tissue can be recognized. These are loose "vascular" connective tissue and dense connective tissue. Between these extremes, intermediate forms occur. The loose "vascular" connective tissue (Fig. 14) is characterized by an open network of slender fibroblasts which, in section, appear as numerous oval or irregularly round perforations, the "*Zirkulationslücken*" of Kisker (1923). These perforations, or circulation spaces, hold the hemolymph of the snail, which stains a homogeneous pink with eosin Y (Fig. 14 a). Few additional cellular and fibrillar elements are present in this type of connective tissue. So-called "concretions" occur in the meshworks. These are crystalline-like structures of irregular shape and size (Fig. 14 c) and stain light blue with hematoxylin or light pink with PAS. The loose "vascular" connective tissue is found characteristically in the dorsal wall of the coelomic cavity, in the pseudobranch, the liver and the ovotestis (Figs. 6, 7, 9).

The dense connective tissue contains numerous fibroblasts, pigment cells and some amoebocytes as well as large amounts of collagenous-like fibers. There is no fibroblastic meshwork, but the cellular and fibrillar elements are embedded in the ground substance to form a compact tissue mass. Smooth muscle fibers are also abundant in this type of connective tissue. Since the ground substance, fibroblasts and collagenous-like fibers all stain pinkish blue in hematoxylin-eosin preparations, the ground substance may obscure the cytoplasm of the fibroblasts and also the collagenous-like fibers. *"Zirkulationslücken"* are present, but they are small in size and number and are inconspicuous. The dense connective tissue is seen characteristically in the foot proper and in the core of the tentacles (Fig. 15). Staining of this tissue with aldehyde fuchsin and acid orcein yielded negative results; therefore, as in land pulmonates (Baecker, 1932), *A. glabratus* is without true elastic fibers.

*Fibroblasts.* The fibroblasts of *A. glabratus* appear to have the ability to transform into a variety of cell types and to be involved in the repair of damaged tissues. In section they are fusiform or spindle-shaped but may have several branching processes (Fig. 16). These processes attach to or end on nearby fibroblasts and form the meshwork of the loose "vascular" connective tissue. The elongated or oval nucleus of the fibroblast has a delicate nuclear membrane, one or two nucleoli and moderately rich, fine chromatin. In stained material, the cytoplasm usually appears to be scanty and can be visualized only at the poles of the nucleus. It stains an almost homogeneous, light pinkish blue in hematoxylin-eosin preparations.

Various amounts of brown to brown-black pigment are frequently seen in the fibroblasts; and since intermediate forms may be seen, especially in pathological tissue (Fig. 17), it is considered that pigment cells may be derived from fibroblasts. The possible transformation of fibroblasts into amoebocytes will be described later.

*Pigment cells.* These cells approximate 15 x 21 microns (Fig. 17). They are very irregular in shape, being round, oval or elongated, and may bear processes, as described for this type of cell in land pulmonates by Baecker (1932). The nucleus is also irregularly shaped, may be round, oval or lentiform and is

frequently eccentric with relatively rich chromatin. The cytoplasm contains acidophilic granules which may be obscured or completely replaced by brown to brown-black coarse pigment granules. These pigment granules react to various stains similarly to the pigment of the epithelial cells. While pigment cells are distributed throughout the connective tissue, they are especially abundant in the rectal ridge and the renal ridge, and in pathological tissues. They may derive from fibroblasts as described in the preceding section. Their presence in large numbers was frequently connected with certain microbial infections (Pan, 1956). Marcuzzi (1950) described the pigment cells in *A. glabratus* as being excretory in function. Stein and Mackin (1955) reported that increased numbers of pigment cells, in oysters, were associated with certain infections.

*Vesicular cells.* Baecker (1932) described and discussed vesicular cells (*Blasenzellen*) in land pulmonates. Carriker and Bilstad (1946) found them in *Lymnaea stagnalis appressa*. These cells are irregular in shape, being round, ovoid, elongate and spindle-form, and measure up to 70 x 35 microns (Figs. 18, 52). The nuclei are relatively small, quite regular in shape, usually round or oval, and contain few chromatin granules. Binucleated cells are seen frequently. The nuclei are often eccentric and may be attached to the cell membrane. The cell membrane usually is discrete and stains well with eosin, aniline blue or fast green. The characteristic homogeneously-staining cytoplasm may contain a fibrillar network which stains less intensely than the plasma membrane, and reacts strongly with PAS suggesting the presence of carbohydrate material. In hematoxylin-eosin preparations the cytoplasmic mass may appear condensed around the nucleus, thus creating a space in the cytoplasm. The vesicular cells are distributed in many parts of the body; they form small groups in the radular carrier and the dorsal wall of the buccal cavity (Figs. 49, 52). The connective tissue of the liver and ovotestis also contains many of these cells.

Schaeffer (Baecker, 1932) postulated that the vesicular cells serve primarily as elastic supporting structures due to the fluid contents enclosed in the thick cell membrane. Since they occur in large numbers in the radular carrier and in the dorsal wall of the buccal cavity, they appear to have this supportive function.

However, the large amount of PAS-positive material also suggests other functions, such as the storage of carbohydrates. This latter function may be especially important in the connective tissue of the liver and ovotestis where it is probably connected with digestion and gametogenesis respectively, as suggested by Faust (1920).

*Mucous cells.* Scattered, well-developed mucous cells occur in small numbers throughout the connective tissue proper in *A. glabratus.* They are also found concentrated in large numbers in two glands: (a) a foot gland and (b) a buccal gland. The buccal gland will be described in the section on the alimentary system. Unlike the land pulmonate (Baecker, 1932), the foot gland of *A. glabratus* does not have an excretory duct. Each mucous cell comprises a secreting unit and secretes mucus through a gradually tapering process (Fig. 19). The cell is usually teardrop or retort-shaped but may be pleomorphic. In size these cells vary considerably but usually measure about 23 microns at the widest diameter. The relatively round or oval nucleus is extremely rich in chromatin and possesses an eccentric, large nucleolus. When the cells are filled with secretion materials, the nuclei tend to lose their normal structure and become pyknotic. As has been described by Baecker (1932) and Carriker and Bilstad (1946) in other species, these cells contain various cytoplasmic structures depending on the stage of secretory activity. In hematoxylin-eosin preparations, the cytoplasm of actively secreting cells is filled with large basophilic granules which usually obscure the nucleus. These basophilic granules are strongly PAS-positive but do not show metachromasia with thionin or toluidine blue O. They stain with orange G in Mallory's trichrome stain. After the secretory materials are released, the cytoplasm loses the basophilic substance, becomes finely reticular, and shows only weak reaction to PAS stain. In the foot gland, several of the mucous cells form subgroups, and the secreting processes bundle together and extend toward the epithelial sheet. The muscle fibers of the foot run through and between the subgroups. These muscles probably serve to force the secreted mucus through the intercellular spaces of the epithelial cells.

*Collagenous-like fibers.* The connective tissue fibers of land pulmonates resemble the collagenous fibers of higher animals (Baecker, 1932) and are described as collagenous-like fibers from *Lymnaea stagnalis* by Carriker and Bilstad (1946). In *A. glabratus* these fibers are more delicate than the muscle fibers, and are differentiated poorly in hematoxylin-eosin preparations taking a light pinkish-blue hue. They are colored blue by Mallory's triple stain and green by Gomori's trichrome, but they are not impregnated by Bielschowski-Glees' or Bodian's silver stain. They are more abundant in dense connective tissue than elsewhere. Fibers seen in the basement membrane of epithelial sheets are more delicate than the collagenous-like fibers in the connective tissue proper. The staining reaction of both types is similar.

*Delicate fibrils on the individual muscle fibers.* Baecker (1932) described delicate fibrils (*"Gitterfasern"*) lying on the surface of sarcolemma of land pulmonates; these can be stained with aniline blue or by silver impregnation. The perimycium of *A. glabratus* contains similar fibers which encircle the muscle fibers. Although they stain with aniline blue in Mallory's trichrome, silver impregnation fails to stain them. They are extremely delicate and recognizable with difficulty unless special stains are employed. From the staining characteristics, these fibrils are probably modified collagenous-like fibers.

## III. Muscular Tissue

It has been pointed out by Olson (1942) that although the muscle fibers of the molluscs have been much studied, there is yet no real agreement as to their structure. Baecker (1932) summarized the work of previous investigators and stated that two types of muscle fibers, smooth and striated, are present in land pulmonates, and that the latter is a very primitive type. Marcuzzi (1950) described both smooth and striated muscle fibers in *A. glabratus*. We observed three different types of muscle fibers in our preparations, but we have not been able to observe fibers which possess periodic striations comparable to those of higher animals. Baecker (1932) pointed out that

the muscle of land pulmonates does not react to stains exactly as that of the higher animals, and in this respect the muscle fibers of molluscs are regarded by him as somewhat related to collagenous-like fibers of connective tissue. This is also true in *A. glabratus*, in which muscle fibers, especially smooth fibers, may occasionally stain as do collagenous-like fibers. Thus, some of the smooth fibers or portions of smooth fibers may stain with fast green in Gomori's trichrome or with aniline blue in Mallory's triple stain instead of with Chromatrope 2 R or Orange G respectively.

The three types of muscle fibers observed in *A. glabratus* are (a) granular muscle or heart muscle, (b) intermediate granular muscle, and (c) smooth muscle.

*Granular muscle or heart muscle.* Marcuzzi (1950) reported that the heart muscle of *A. glabratus* is of the obliquely striated type of Plenk (1924). We could not demonstrate striations (cross, or oblique) in the muscle fibers of this organ by any of the ordinary cytological techniques (iron hematoxylin, phosphotungstic acid hematoxylin, toluidine blue O, hemalum, phloxine B and eosin Y). In cross-section the fibers appear round, oval, angular or irregular in shape. The fiber is enveloped by a delicate, somewhat refractile membrane (plasmalemma or sarcolemma) which stains lightly basophilic. The fibers measure $\pm 12$ microns in thickness. No myofibrils could be recognized, but the fiber is filled with relatively coarse acidophilic granules. These granules are distributed quite evenly within the fibers, but may at times be concentrated in the peripheral zone (Fig. 20). Occasionally these granules are seen to be connected by very delicate fibrils.

In longitudinal sections (Fig. 20) the fiber is spindle-shaped with a thickened mid-portion at the site of the nucleus. The coarse acidophilic granules also are more or less concentrated in the peripheral zone. Myofibrils were not recognized in the longitudinal positions. The nucleus is single, round to oval in shape and has but little chromatin. There is no clear area around the nucleus, as occurs in vertebrates. The heart muscle fibers of *A. glabratus* anastomose freely to each other as in vertebrates, but there are no intercalated discs. Connective tissue is scarce, and the fibroblasts attach here and there on the muscle fibers.

The fibroblasts sometimes contain a small amount of brown granular pigment. There is no true endocardium, but the outer surface of the heart is protected by a well-developed epicardium (Figs. 33, 35).

This type of granular muscle fiber is seen only in the heart of *A. glabratus*. Infrequently the granules in some fibers may be so arranged that striation is suggested. Marcuzzi (1950) apparently observed this condition. The heart muscle of *A. glabratus* forms only primary bundles.

*Intermediate granular type of muscle.* This type of fiber is apparently an intermediate form between the granular muscle (heart muscle) and smooth muscle, and is confined to the buccal mass. It may measure up to 10 microns in thickness. In cross-section the muscle fibers appear more irregular in shape than in heart muscle and present round, oval, triangular and quadrangular outlines. There are two clearly defined zones: a rather heavily stained peripheral zone and a lightly stained central zone (Fig. 21). The refractile sarcolemma is thinner than that of the heart muscle. Delicate myofibrils are evenly packed in the peripheral zone and stain intensely acidophilic. The central zone contains a number of coarse granules which are stained less acidophilic than the myofibrils.

In longitudinal sections (Fig. 21) the fibers are spindle-shaped, having a slightly thickened middle portion. Myofibrils run parallel to the long axis of the fiber in the more heavily stained peripheral zone. The inner portion stains lightly acidophilic and contains evenly scattered, coarse granules which occasionally may be linked with fine threads. The granules are, as in the case of heart muscle, arranged at times so as to show an irregular, cross-striation-like appearance. This striated appearance is not constant and when it does appear in a preparation only a few such fibers show it. Each fiber contains one centrally-located nucleus at the thickened middle portion of the fiber. The nucleus is oval, poor in chromatin granules and usually possesses a nucleolus. This type of muscle fiber has been described for many molluscs by various authors, especially by Olson (1942) who studied it in the radular retractor of *Busycon* sp.

The muscle of the buccal mass forms primary and secondary bundles. Small amounts of endomysium bind individual fibers to form primary bundles which are in turn bound by perimysium to form secondary bundles. These interstitial tissues are collagenous in nature and can be stained with PAS, Mallory's or Gomori's trichrome stains. Fibroblasts may attach on the surface of sarcolemma and may contain brown pigment granules.

*Smooth muscle.* This type of muscle cell is comparable to that of vertebrates and constitutes the major musculature of *A. glabratus*. It is found in the columellar muscle, foot muscle, alimentary canal, genital tracts, tentacles, and other areas. Its fibers are the smallest of the three muscle types, measure less than 9 microns in thickness, and show considerable morphologic variation.

In cross-section the fibers appear round to ovoid or angular in shape. In longitudinal sections they are fusiform with a thickened mid-portion containing the nucleus. The fibers stain uniformly acidophilic and do not contain granules except rarely about the nucleus. Myofibrils are abundant and can be recognized readily running along the long axis of the fibers in properly fixed specimens (Fig. 22). They are distributed evenly in the fibers and are packed together tightly. A sarcolemma cannot be recognized as such, but a very thin, refractile outline surrounds the fiber.

The single nucleus is elongate or oval. It lies along the long axis of the fiber and is somewhat eccentric in position. There is usually a nucleolus; the chromatin granules are small and few. Dark brown pigment may be present around the nucleus, especially at its poles.

Most of the fibers in the foot run singly in various directions through the dense connective tissue. In the columellar muscle the fibers form primary and secondary bundles which run along the long body axis. The endomysium and perimysium are more abundant here than in the buccal mass musculature.

## IV. Nervous System and Sensory Organs

The nervous system of *A. glabratus* consists of central ganglia, peripheral ganglion, individual ganglion cells, and nerves. The sensory organs observed in this study are: statocysts, eyes,

osphradium, tentacles, and five groups of small sensory cells, one each at the base of each tentacle and the margin of each lip respectively.

*Central ganglia.* According to Baker (1911 and 1945) and Baecker (1932) the central ganglion ring of pulmonate snails is characteristically composed of 11 separate ganglia which are linked by communicating branches of commissures to form a ganglion ring around the esophagus immediately behind its union with the buccal mass. There are two cerebral ganglia above the esophagus, and below the esophagus there are two buccal ganglia, two pedal ganglia, two pleural ganglia, two visceral ganglia and a single abdominal ganglion (Baker 1945).

The arrangement of the ganglia in *A. glabratus* is essentially the same as in other pulmonate snails. The paired visceral ganglia are not of equal size, the left ganglion being somewhat larger than the right one. All of the parallel ganglia and their commissures are covered by a common connective tissue sheath, the epineurium. Histologically, these ganglia are similar in arrangement and composition (Figs. 2, 6, 23). The epineurium is a relatively thick connective tissue layer which is rich in cellular and fibrous elements. The collagenous-like fibers are relatively coarse, loosely packed, and, for the most part, run parallel to each other along the long axis of the ganglion. A few cross fibers are also present. The cellular elements are similar to the fibroblasts of the connective tissue. Each ganglion is directly covered by a sheath, one cell thick, the perineurium. It stains more intensely than the epineurium with connective tissue stains such as Mallory's or Gomori's trichrome. Arteries and blood spaces are present in the epineurium. Vesicular cells seen in the epineurium of land pulmonates by Baecker (1932) were not observed in the ganglia of *A. glabratus*.

Ganglion cells (Figs. 6, 23, 24) are located on the periphery of the ganglia and many are in contact with the perineurium; however, areas where the nerve root and commissure leave a ganglion are devoid of ganglion cells. The center of the ganglion contains neurofibrils sent out by the ganglion cells and is thus filled with neurofibrils which run in various directions in bundles.

A few fibroblast-like slender cells occur among these neurofibrils in the ganglion and larger nerves. These cells under pathological stimuli may become hyperplastic and phagocytic and apparently are equivalent to the glia cells of the vertebrate central nervous system.

According to Nabia (Baecker, 1932) two types of ganglion cells are present in the gastropod nervous system; one, the so-called ordinary ganglion cell with a relatively large amount of cytoplasm, and the second, the chromatinic ganglion cell, with sparse cytoplasm and of small size. In *A. glabratus* the chromatinic ganglion cells form two prominent groups in the dorsoposterior corner of each cerebral ganglion. The nuclei of these cells, measuring 7 x 4 microns, are slightly larger than those of fibroblasts, and the cytoplasm is seen as a small rim around the nucleus. The so-called ordinary ganglion cells may measure 59.5 x 52.5 microns, with nuclei of 42.0 x 24.5 microns. The nucleus has a definite nuclear membrane, contains a large number of coarse chromatin granules held in a linin network, and one or two nucleoli (Fig. 24). The nucleolus is located eccentrically and may be oval. The cytoplasm contains a large amount of basophilic material in the form of coarse granules or small plaques (especially in thionin-stained preparations) which resemble Nissl's bodies in the vertebrates. Although silver impregnation (Bielschowski-Glees' and Bodian's method) was not successful in impregnating neurofibrils, many of the Bouin-fixed preparations, when overstained with hemalum, contained fibrillar networks in the cytoplasm of the larger ganglion cells. Neuroglia cells may surround the larger ganglion cells, but none of them was observed inside the cytoplasm of ganglion cells (i.e., the "*Trophospongien*" of Holmgren, 1905). The structure of the central ganglia, as described above, is somewhat similar to the central nervous system of higher animals in that the neurons are located in the peripheral zone (gray substance) and the neurofibrils are concentrated in the central zone (white substance). Baecker (1932) also pointed out this correlation in the central nervous system of land pulmonates. However, myelinated nerve fibers were not demonstrated in *A. glabratus;* neither were they seen in land pulmonates by Baecker (1932).

This author also described neuroglia cells in the ganglia of land pulmonates and observed that the cells were concentrated in the peripheral zone of the ganglia. In *A. glabratus*, neuroglia cells are similar morphologically to fibroblasts and are scattered evenly in the ganglia in small numbers (Fig. 23). Hyperplasia and transformation of neuroglia into phagocytes were observed in a few snails which were infected with an unidentified yeast-like organism. In some instances partial or complete replacement of ganglion cells and neurofibrils of affected ganglia by neuroglia was also observed (Fig. 25).

*Peripheral ganglion cells and peripheral ganglion.* Peripheral ganglion cells are scattered singly or in small numbers in various organs and tissues. These cells are morphologically similar to those in the central ganglia. There appears to be only one peripheral ganglion present in *A. glabratus*. This ganglion is associated with the osphradium (Fig. 29) and will be described later.

*Nerves.* The structure of the nerve in *A. glabratus* resembles that of the *Helix* nerve described by Baecker (1932). The bundles of neurofibrils are covered by the connective tissue sheath (peri- and epineurium) of the ganglion in the root area. The perineurium is lost shortly below the ganglion. The epineurium is continuous with that of the ganglion and is relatively thick in the larger nerves. In small peripheral nerves the epineurium becomes one cell thick and has only a few collagenous-like fibers. Most of the fibers run along the long axis, but circular fibers are also present. These stain light blue with Azan triple stain, green with Gomori's trichrome, and pinkish-blue with hematoxylin-eosin. The neurofibrils stain bluish-red and dark red with Mallory's and Gomori's trichrome respectively. Neuroglia cells are present among the neurofibrils and are more abundant in larger nerves. They are usually spindle-shaped and run with or obliquely to the long axis of the nerve (Fig. 26). No myelinated neurofibrils were observed in *A. glabratus*. The nerve trunks and large nerves of *A. glabratus* can be recognized without difficulty in hematoxylin-eosin preparations by their staining characteristics and structures. In cross-section of the larger nerves a connective tissue substance may form incomplete septa

at the periphery. Since no myelinated neurofibrils were demonstrated in *A. glabratus,* the nerve of this snail belongs to the "incomplete type" of Schultze (Baecker, 1932). The axis cylinders, or neurofibrils, in individual nerves, are embedded in a ground substance which takes up fast green or aniline blue.

*Statocyst.* The statocyst, or the balancing organ of the pulmonates, has been described in detail for the genus *Helix* by Baecker (1932). The statocyst in *A. glabratus* appears to have structures similar to those of *Helix.* In *Australorbis* it is a paired organ located in the latero-posterior corner of each pedal ganglion at the root of the commissure to the pleural ganglion. It is an oval-shaped sac measuring approximately 94.5 x 66.5 microns (20 x 6.4 mm. snail )and lies embedded in the epineurium of the pedal ganglion (Fig. 23). Unlike *Helix,* the main nerve to the statocyst of *A. glabratus* originates from the pedal ganglion, but it also receives a smaller nerve from the pleural ganglion. The wall of the statocyst consists of (1) an outer layer, (2) a middle layer and (3) an inner or epithelial layer. The outer layer is a connective tissue sheath, rich in circular collagenous-like fibers, and is fused into the epineurium of the pedal ganglion. The middle layer is a very thin homogeneous capsule which can be recognized only with a connective tissue stain. It is considered by Baecker (1932) to be the basement membrane of the epithelial layer in *Helix.* The inner or epithelial layer is composed of two types of epithelial cells which intermingle and form a membrane one-cell thick. One type of cell is small, flat and fibroblast-like with chromatin-rich nuclei but with little cytoplasm and indistinct boundaries. The other type includes cells which are half-moon in shape with the convex side on the basement membrane. They usually measure 25 x 12.5 microns and are the "giant cells" of Baecker (1932). The nucleus is small, oval, and is somewhat peripherally situated. On the basal side of the nucleus, the basophilic cytoplasm may contain large vacuoles supported by fibrillar structures. Neurofibrils may be traced into the cytoplasm of these larger cells but are not present in the smaller or first type. The free surface of the "giant cells" is covered with long, but sparse, cilia. The lumen of the statocyst sac contains ovoidal bodies, the statoliths. They measure 4 x 3 microns and stain lightly basophilic (Fig. 24). The peripheral zone appears denser than the central zone.

*Eyes.* The eyes of pulmonates are well developed and are comparable in structure to those of vertebrates. Smith (1906) made a detailed study of the eyes of pulmonates, and the more recent studies are summarized by Baecker (1932). According to the former author, land pulmonates have the following eye structures: optic capsule, cornea, retina, lens, vitreous humor, optic nerve and accessory retina.

The eyes of *A. glabratus* are located latero-posteriorly to the base of each tentacle and are embedded in the dorsal wall of the head. All of the above-mentioned eye structures for pulmonates, except the accessory retina, were recognized in *A. glabratus* (Fig. 27). In addition, a few delicate smooth muscle fibers were observed to be attached to the optic capsule.

The optic capsule consists of a connective tissue sheath which is one cell thick on the surface of the cornea, but becomes two to three cells thick near the optic nerve where it fuses with the epineurium or connective tissue sheath of the latter. The cornea and retina together form a closed sac which constitutes a wall, one cell thick, enclosing the lens and the vitreous humor. Between the cornea and the epithelium of the head there is a small space which is filled with tissue fluid and contains a few wandering cells or amoebocytes. The cornea is of non-pigmented, squamous epithelium and is in close contact with the lens on the inner surface and with the optic capsule on the outer surface. It covers approximately one-third of the surface of the eyeball.

The retina (Fig. 27) makes up the remaining portion of the sac. As shown for *Planorbis trivolvis* by Smith (1906), there are three differentiated regions in the layer of simple epithelium. The outer zone is in contact with the optic capsule and comprises the non-pigmented but nucleated portions of the retinal cells. The middle region consists of the constricted portions of the sensory cells and the pigmented portions of the pigmented or supportive cells. The sensory cells in this region are usually obscured by the heavily pigmented, thick cytoplasm of the pigment cells. The inner zone is made up of the rods of sensory cells and is in contact with the vitreous humor. Both types of retinal cells (the sensory and the pigment) are attached to the optic capsule by radiculae (Smith, 1906). The pigment cells are

more slender and basophilic than the sensory cells at the peripheral zone. The nuclei of the pigment cells generally are nearer the capsule and are smaller than are the nuclei of the sensory cells.

The rods constitute those portions of the sensory cells which extend beyond the middle pigment zone, and are light receptors according to Smith (1906). In the P.F.F.-fixed and hematoxylin-phloxine B-stained preparations, the rods appear as club-shaped objects surrounded by a radially striated thick mantle.

The lens is spheroidal, occupies most of the ocular sac, and is strongly acidophilic. The peripheral zone of the lens is homogeneous, but the central zone is porous, perhaps an artifact due to fixation and staining. The vitreous humor is very small in amount and stains lightly pink.

The optic nerve originates from the cerebral ganglion and has the structure of a medium-sized nerve.

*Osphradium.* Baecker (1932) did not describe the osphradium, or the so-called olfactory organ, as occurring in land pulmonates. The osphradium in *A. glabratus* is located where the mantle collar joins the neck of the snail between the median line and the pneumostome siphon (Fig. 1 f). It is a somewhat elongated pear-shaped sac, about 300 x 120 microns in a snail measuring 15 x 5.1 mm. The opening of the osphradium is obscure in living specimens. In section, the lumen is lined with a layer of tall columnar epithelial cells covered with long, dense cilia (Figs. 28, 29). Two types of columnar epithelial cells can be identified. One has a basal oval nucleus which is rich in chromatin, and the cytoplasm is filled with basophilic granules. The second type is a slender cell compressed between cells of the former type and has a central elongated nucleus. The cytoplasm is scanty and cannot be clearly recognized. The epithelium of the osphradium is replaced by the cuboidal cells of the neck and mantle surfaces at the opening to the exterior. The epithelium rests directly on a layer of smooth muscle fibers (mostly circular and some longitudinal) that contain a few fibroblasts (Fig. 28). The lower portion of the sac is surrounded by a peripheral ganglion (Fig. 29). The structure of this peripheral ganglion is similar to that of the central ganglia. Neurofibrils from these ganglion cells

appear to penetrate through the muscle layer and end on the epithelial cells. The ganglion attached to the osphradium receives a thick branch nerve from the left visceral ganglion.

*Tentacles.* There is but one pair of tentacles in *A. glabratus.* The tentacle is the most abundantly innervated and the most flexible structure of the snail. Thus, it is a very delicate tactile sense organ. A thick nerve trunk arises from the cerebral ganglion and, after reaching the root of the tentacle, passes through the central core of the tentacle to the very tip. Anatomically, the tentacle is a gradually tapering cylinder. On the cross-section it has a round contour except at the base where there is a leaf-like enlargement on the lateral side (Fig. 30). The core of the tentacle near the root consists of dense connective tissue which becomes less dense toward the tip. A central artery runs up the core to the tip where it empties into the peripheral blood sinuses. The connective tissue of the core sends out radial strands of fibroblasts to the epithelial sheet (Fig. 31). The nerve trunk is embedded in this core of connective tissue and also sends out many branches to the epithelium along the radial connective tissue bridges; the bridges also contain delicate muscle fibers. Longitudinal muscle fibers and pigment cells are abundant in the central connective tissue core. The hemolymph fills the interstices between the central core and the peripheral epithelium. The simple short columnar-covering epithelium bears dense cilia. The basement membrane is not distinct toward the tip. Beneath the basement membrane there are a few delicate circular muscle fibers intermingled with fibroblasts. Postulating from the histological structure, the extension of the tentacle is probably accomplished by the filling of the blood sinuses with hemolymph through the central artery. The retraction of the tentacle is apparently accomplished by the contraction of the longitudinal and circular muscle fibers with resultant emptying of the hemolymph from the sinuses.

*Sensory cells at the margin of the lips and at the bases of the tentacles.* There are five specialized groups of sensory cells, one associated with each leaf-like enlargement at the base of the tentacle and one at the margin of each lip. These cells are subdivided into many clumps by fibroblasts and are in close contact with the basement membrane (Fig. 32). They resemble the

chromatinic ganglion cells of the central ganglia. These sensory cells are short, fusiform in shape, contain chromatin-rich ovoid nuclei and have a very basophilic, vacuolated cytoplasm. One end of each fusiform cell fuses into the bundle of neurofibrils sent out from the branches of the nerve innervating the tentacle. The other end of the cell is directed peripherally and tapers off into a filament. Many of these cells are in direct contact with the epithelial cells of their respective areas. Although the exact nature of these cells is not clear, they appear to function as peripheral sensory cells.

## V. Circulatory System

According to Baker (1945) the circulatory system of planorbid snails consists of a heart, arterial system, venous system, and blood sinus system. Histological description of these organs in land pulmonates is given by Baecker (1932).

Our histological studies of the circulatory system of *A. glabratus* fully agree with Baker's anatomical observations. However, the "loose vascular" connective tissue should be mentioned as an integral part of the circulatory system.

*Heart.* The heart consists of two chambers: a caudal pear-shaped, muscular ventricle, and a cranial pear-shaped, thin-walled atrium. These two chambers are joined at their wide bases by a constriction where there is a pair of muscular valves (Fig. 33). The valves are directed into the ventricle and are thin muscular sheets covered by cells resembling those of the epicardium. The junction between the ventricle and aorta is also provided with a thin muscular valve which is directed into the aorta (Fig. 34). The muscle of the heart is of the granular type already described.

The atrium has a very thin muscular wall and is more distensible than the ventricle. In sectioned material the lumen of the atrium is usually several times larger than that of the ventricle.

The thick muscular wall of the ventricle is formed by a three-dimensional mesh of branching and anastomosing muscle fibers, slightly more densely woven adjacent to the epicardium. The wall of the heart (both chambers) consists principally of longitudinal and circular muscle fibers. Some of the branching fibers

form trabeculae that cross the lumen to the opposite wall. Fibroblast-like, fusiform cells occur among the muscle fibers and are especially prominent in certain pathological conditions. In *Helix,* Baecker (1932) regarded these fusiform cells as perimysium and not as endocardium. There appears to be no true endocardium in *A. glabratus.*

The outer surface of the heart is covered with a continuous layer of cells which comprise the epicardium (Figs. 33, 35). These cells are round to short, columnar in shape, with distinct boundaries when the heart is contracted, but become flat and without clear boundaries when it is distended. In the contracted position of the heart, the nuclei of the epicardial cells are round to oval, subbasal in position and poor in chromatin granules. The cytoplasm is finely or coarsely vacuolated and contains basophilic filamentous material (Fig. 35). The structure of the epicardium appears to be adapted for great distention.

The heart is enclosed in the pericardial sac which is connected to the lumen of the saccular portion of the kidney by a renopericardial canal (see section on kidney) (Fig. 46). The pericardial sac is bordered by a portion of the saccular kidney, part of the mantle and by membranous tissue which is an extension of the mantle into the mantle cavity. The internal surface of the sac is lined by a sheet of flat cells which contain a moderate amount of dark brown pigment.

*Arteries.* In large arteries, including the aortae, the wall is composed of three layers (Figs. 36, 37). The lumen is lined with a layer of fibroblast-like cells which are very thin and barely recognizable under most conditions. Baecker (1932) stated that these lining cells as well as the connective tissue cells of the heart, are not truly endothelial in nature. From our observations in *Australorbis,* these cells may undergo hyperplasia and hypertrophy under pathologic stimuli; they then may become detached and transformed into phagocytes (Figs. 36, 40). Therefore, we believe these lining cells bear endothelial properties. Beneath the lining cells there is a layer of smooth muscle fibers, most of which are circular, but longitudinal fibers are also present. The muscular layer is covered with a varying amount of connective tissue. In small arteries the muscle and connective tissue layers may be absent, but the lining cells are well defined.

*Veins.* The veins have no definite wall and are tissue spaces which are lined incompletely with fibroblast-like cells (Fig. 38); thus the veins cannot be differentiated from the surrounding tissues. The veins connect freely with the blood sinus system.

*Blood sinuses.* The blood sinuses are tissue spaces which are interlaced abundantly by fibroblasts, some of which form a trabecula-like support. The most conspicuous blood sinuses are those in the mantle (Fig. 39).

The blood or hemolymph appears to be forced into the "loose vascular" connective tissue via arteries, and after bathing the organs and tissues is collected in the blood sinuses. It is finally returned to the atrium of the heart via the pulmonary and renal veins. Both of these veins pass along the lateral sides of the kidney and unite near the blind end of the saccular portion of the kidney before entering the atrium of the heart. The hemolymph in the "loose vascular" connective tissue is apparently squeezed forward by the smooth muscle fibers present in that tissue, as described by Baecker (1932). Our description of the vascular system of *A. glabratus* essentially agrees with that given by Baecker for land pulmonates. However, hyperplasia and transformation of the lining cells into amoebocytes are probably noted for the first time in the pulmonate snails.

*Amoebocytes or wandering phagocytes.* In *Helix*, Baecker (1932) described nucleated blood corpuscles which he regarded as equivalent to the leucocytes in higher animals; he called these nucleated blood corpuscles "*Amoebocyten*" and these were said to have phagocytic functions. In *A. glabratus,* only nucleated blood corpuscles occur and these cells closely resemble the amoebocytes described by Baecker in *Helix* (Fig. 40). Several kinds of amoebocytes have been described in molluscs by various workers (George and Ferguson, 1950; Wagge, 1955). Although there may be different types in *A. glabratus* we did not attempt their differentiation, and the nucleated cellular components of the hemolymph are all included as amoebocytes. They occur in small numbers in the circulatory system as well as in connective tissue. Because of the semi-open circulatory system of *A. glabratus*, the amoebocytes are normally fairly evenly distributed in the connective tissue, but in certain pathological states a large number may localize in diseased tissue areas (Fig. 41). In one type of

inflammatory reaction observed, a large number of microorganisms were present in the cytoplasm which then became rounded and enlarged from two to three times its normal size (Fig. 42). In sections, the amoebocyte of *A. glabratus* measures approximately 9 x 12 microns, but there is considerable variation in size and shape. However, many are round or oval with occasional lobose pseudopodia. The nucleus is vesicular, and round, oval or lentiform. It contains a moderate amount of coarse granular chromatin and is usually eccentric in position (Fig. 40). The cytoplasm is lightly basophilic and granular and usually shows coarse vacuolation.

*Hemopoietic tissues.* According to Baecker (1932), the origin of the amoebocyte in land pulmonates is unknown. However, recent workers have observed that the fibroblasts and epithelial cells of the mantle in *Helix* sp. transform into amoebocytes under certain conditions (Haughton, 1934; Crawford and Barer, 1951; Wagge, 1951, 1955). No mention of specially differentiated hemopoietic tissues was made by these workers. Haughton (1934) indicated that the blood vessels in the invertebrates were the place of origin of the amoebocytes. Our observations suggest that possible normal sites of production for amoebocytes are the blood sinuses and the wall of the saccular portion of the kidney which forms part of the pericardial sac. The fibroblasts which form the trabecula-like supports of the blood sinuses in the mantle frequently round up, but remain attached to the wall of the sinus by a cytoplasmic process. The typical elongated nucleus of the fibroblast is lost in this transition form and becomes vesicular as in the mature amoebocyte. The wall of the saccular portion of kidney bordering the pericardial cavity is composed of primitive tissue probably of mesenchymatous origin (Fig. 43). The cellular components are round or oval in shape but with irregular outlines and with processes which join with those of the neighboring cells to form a cellular reticulum. They are fairly closely packed and imbedded in a ground substance which contains some collagenous-like fibers. The cytoplasm is lightly basophilic, may contain several vacuoles, and in general closely resembles that of the mature amoebocyte. The nuclei are vesicular and also resemble those of amoebocytes. Mitotic figures are frequently seen in this tissue. The cellular reticulum has numerous blood spaces

which are connected with the blood sinuses of the saccular portion of the kidney. The appearance of this tissue resembles closely the medulla of lymph nodes in the vertebrates. Extreme hyperplasia in this tissue was noted in certain pathological conditions and the cellular components were observed to contain many microorganisms. Amoebocytes free in the blood spaces were regularly seen in this tissue. From its histological structure as well as its behavior in pathological states, this tissue may be regarded as hemopoietic tissue or lymphoid tissue, and it is described for the first time in this study.

In pathologic conditions, the fibroblasts in various parts of the body of *A. glabratus,* especially the rectal ridge and the kidney ridge, were also observed to participate in production of amoebocytes. Under such circumstances transition forms are frequently noted in the connective tissue.

Although the amoebocyte has been described by various authors as being concerned with digestion and with the repair of damaged shells (Yonge, 1946; Wagge, 1951; George, 1952; Wagge and Mittler, 1953), we found little activity of amoebocytes in *A. glabratus* which may be correlated with these functions. We observed few amoebocytes around the digestive tract of this snail. The main activity of the amoebocytes in *A. glabratus*, according to our observations, appears to be phagocytosis of foreign bodies, especially microorganisms.

## VI. Respiratory System

The respiratory system of *A. glabratus* consists of a pneumostome equipped with a pneumostome siphon (pseudobranch), and the mantle cavity. The pneumostome is surrounded by a portion of mantle collar and the neck. It is loosely divided into two openings by the pseudobranch which protrudes out of the mantle cavity. The pneumostome siphon occupies the right opening and is actually a curled, small flap of tissue arising from the neck and possessing a moderately loose vascular connective tissue, as stroma. The epithelial cells of the mantle collar and the siphon are cuboidal to short columnar in type. In the stroma of these structures, pigment cells and smooth muscle fibers are present in moderate amounts.

The wall of the mantle cavity is provided with three ridges which protrude into the lumen and apparently serve to increase the respiratory surface. These are the kidney ridge, rectal ridge, and the dorsal ridge which is situated between the kidney ridge and the rectal ridge on the left side. The first two ridges contain two veins each and the dorsal ridge contains one vein. In each case, the veins run along the long axis of the ridge. Although the epithelium in the mantle cavity serves as respiratory epithelium, no special differentiation of these cells from the other, non-respiratory epithelia could be recognized. The cilia of the tall columnar epithelial cells on the summits of the three ridges apparently serve to guide the flow of water which enters the mantle cavity. The three types of epithelial cells of the mantle cavity surface have been described earlier. Since the supporting connective tissue underlying the basement membrane of the area between the ridges is very thin and the epithelium is therefore in close contact with the blood sinus system, the cuboidal epithelial covering of this area probably has an active respiratory function. Baecker (1932) described this form of respiratory cell in land pulmonates, but the tall ciliated columnar epithelial cells on the summit of the ridges were not mentioned. A few delicate smooth muscle fibers are present beneath the basement membrane. In addition to the veins in the ridges, the mantle is supplied with a bloood sinus system (Fig. 38) which communicates freely with the venous system and is also in intimate contact with the respiratory epithelium.

The three ridges frequently have been observed to be invaded by microorganisms with resulting hyperplasia of fibroblasts and amoebocytes.

## VII. Renal Organ

Baker (1945) described the kidney of the Planorbidae as consisting of a small upper saccular portion, and elongated lower tubular portion, and a short ureter curving nearly 160° to the left before it opened into the mantle cavity at the pneumostome. Baecker (1932) considered the tubular portion of the kidney in land pulmonates as a secondary ureter, while Abdel-Malek (1952) held that both portions of the kidney in Planorbidae are similar

histologically but different anatomically. In *A. glabratus* the two portions of the kidney are histologically and anatomically distinct.

*Tubular portion of the kidney.* The characteristic epithelial cells of the tubular portion of the kidney are low columnar to cuboidal and rest on a thin basement membrane which is supported by a sheet of fibroblasts and a few smooth muscle fibers (Fig. 44). These epithelial cells thus border on the venous and sinus systems and are, therefore, in intimate contact with a rich supply of blood. The epithelial sheet of this portion of the kidney shows an irregular wavy appearance in cross section. The cells are somewhat variable in appearance. In well-fixed material the nuclei are usually round or oval, very rich in chromatin granules and vesicular in type (Fig. 44). They are usually located near the peripheral zone. The cytoplasm is vertically striated from the superior surface to the basement membrane. At times a few small vacuoles may be present in the cytoplasm near the lumen. Again, the vacuoles may be numerous, coalesce to form larger vacuoles, and occupy about two-thirds of the cell. Thus, the nuclei may be forced toward the basement membrane and the acidophilic striations then become delicate, displaced, and confined to the basal third. It is possible that these striations are intracellular canaliculi. The vacuoles contain variable amounts of PAS-positive materials.

The ureter is lined with the same type of epithelial cells as the tubular portion except at the area about the opening where the cells show a transition to the epithelium of the mantle cavity.

*Saccular portion of the kidney.* The wall of the saccular portion forms many prominent folds which run with the long axis of the kidney. The folds may reach the opposite wall. The epithelial cells of the wall of the saccular portion are columnar and are taller than those of the tubular portion but are arranged in the same manner. The folds consist of two epithelial sheets with a blood space between them (Fig. 45). The nuclei are round to oval and are basal in position. In each epithelial cell there is usually a large vacuole which frequently contains a crystalline concretion. The vacuole usually pushes most of the cytoplasm to the basal third of the cell. Unlike the cytoplasm in the tubular portion, the cytoplasm of the cells in the saccular

portion contains coarse acidophilic granules and filamentous material. Little PAS-positive material is present in the vacuoles.

The crystalline concretions were thought by Baecker (1932) to be the urine-substance in land pulmonates. They do not take ordinary stains. They are lightly refractile, round bodies with a central core and appear yellowish-brown in hematoxylin-eosin preparations (Fig. 45). In fresh specimens the presence of numerous concretions gives a yellowish-orange color to the saccular portion of the kidney. The concretions are very weakly PAS-positive.

The lumen of the saccular portion is connected with the pericardial sac by the "renopericardial canal." This canal has been described in *Helix* by Nüsslin and in *Arion* and *Limax* by von Rolle (Baecker, 1932). The canal in *Australorbis* is lined by a sheet of acidophilic cuboidal epithelium at the opening to the pericardial sac. These gradually transform to tall columnar cells toward the renal opening. The free surface of these cells is heavily covered with long cilia (Fig. 46). In specimens prepared in alcoholic fixatives, such as Newcomer's or Carnoy's, and stained with thionin, a few mucous cells may be observed scattered among the epithelial cells.

The mesenchymatous tissue in the wall of the saccular portion of the kidney, which forms part of the wall of the pericardial sac, has been described in the section dealing with amoebocytes.

## VIII. Alimentary System

The histology of the alimentary system in pulmonates has been described in detail by Baecker (1932) and von Haffner (1923) for *Helix* sp. and by Carriker and Bilstad (1946) for *Lymnaea stagnalis appressa*. Baker (1945) described the gross anatomy of the alimentary system of *Australorbis glabratus* and Marcuzzi (1950) studied its histology. In general, this system in *A. glabratus* is comparable to that of *Helix* or *Lymnaea*, but with certain variations.

Morphologically and functionally, the alimentary system of *A. glabratus* can be divided into two parts: the digestive tract and the glandular organs. The digestive tract includes the

buccal mass, the esophagus, the stomach and the intestine. The glandular organs comprise three glands: the buccal, the salivary, and the so-called "liver."

The general structure of the digestive tract is the same throughout, with variations as to size and shape.

The lumen is lined with a sheet of simple columnar epithelium which rests on a basement membrane. The basement membrane is supported by two layers of smooth muscle fibers, an inner longitudinal and an outer circular layer. The thickness of each layer varies considerably. A sheath of connective tissue envelopes the outer muscle layer in the region where the digestive tract lies free in the body cavity.

*Lips and oral cavity.* The oral cavity is bordered externally by three lips, two upper and one lower, located in front of the buccal mass. In cross section, three lips form a "T"-shaped space, which with the buccal mass comprises the oral cavity. The marginal epithelium is composed of ciliated, tall columnar cells like those on the foot surface. These cells are gradually replaced toward the buccal mass cavity by cuticular cells. The cuticular layer which appears bluish-gray and homogeneous in hematoxylin and eosin preparation thickens toward the buccal mass and is transformed into three wedge-shaped horny jaws at the margin of the buccal mass (Fig. 47). The horny jaws stain orange to orange-pink in H-E preparations and appear striped, each stripe arising from individual epithelial cells. Beneath the epithelial sheet is a distinct basement membrane resting on thick dense connective tissue. Delicate smooth muscle fibers run in various directions in the connective tissue. In it are also embedded many mucous cells as well as a group of sensory cells (Fig. 32). A small amount of brown pigment may be observed rarely in the epithelial cells.

*Buccal mass.* The buccal mass, called the "pharynx" in *Helix* by Baecker (1932), functions primarily as a scraping and swallowing organ (Fig. 2). In addition to the complicated muscular layers it contains three distinct structures: i) the chitinous radular ribbon, ii) the radular sac, and iii) the radular carrier. The histology of the muscle of this organ has been described in an early paragraph (see Muscular Tissue). The epithelial

sheet which covers the oral cavity consists of tall columnar cuticular cells except on the floor where interrupted by the radular carrier. The cuticular cells contain centrally located oval nuclei which are rich in coarse chromatin granules (Fig. 48). Many acidophilic striations are present in the slightly basophilic cytoplasm, and these run from the basement membrane to the cuticular layer. They contain larger amounts of coarse granules of brown pigment than do the epithelial cells of the lips. The pigment granules are usually located in the zone between the cuticular layer and the nuclei. The cuticular layer appears bluish-gray in H-E preparation, is strongly positive with PAS-stain, and decreases gradually in thickness toward the esophagus where it is replaced by cilia. A group of vesicular cells which resemble those of the radular carrier is embedded in the dorso-anterior wall of the buccal mass and probably serves as an elastic cushion (Fig. 49). These cells will be described in a later paragraph.

*Radula.* The radula, a structure of taxonomic value, is a serrated chitinous ribbon originating in the radular sac. It passes forward on the floor of the buccal mass toward the lower lip and terminates near the horny jaw. The radular ribbon is supported by the odontophoral cartilage (or radular carrier) which acts as an elastic cushion to control its movement along with the radular protractor and retractor muscles. The radula consists of two parts, the serrated chitinous dentins, and a thin basal plate. The histology of the radula of *Australorbis* is essentially similar to that of *Helix* (Baecker, 1932). The dentins are acidophilic and are embedded in the thin, homogeneous basal plate which is lightly basophilic. A thin layer of connective tissue binds the radular ribbon to the dorsal surface of the radular carrier.

*Radular sac.* The radular sac is located at the ventro-posterior portion of the buccal mass near the junction of the buccal mass and esophagus. In cross section, it is roughly horseshoe-shaped with the convex side facing ventrally (Fig. 50). It is partially embedded in the musculature of the buccal mass and, together with the latter, is covered by a common connective tissue sheath. The radular ribbon is on the periphery and follows the outline of the horseshoe, being held between two sheets of epithelial cells. Both sheets appear to be an extension and modification of the

epithelial sheets of the buccal cavity. The epithelial cells between the radular ribbon and the outer connective tissue sheath consist of a layer of columnar cells (Fig. 51) which, in *Lymnaea stagnalis,* were called the "subradular epithelium" by Carriker and Bilstad (1946). These cells contain central, ovoid nuclei and basophilic cytoplasm and apparently give rise to the basal plate of the radular ribbon. The boundary between the subradular epithelium and the basal plate is largely obscured. Acidophilic striations occur in the cytoplasm in the zone between the nuclei and the basal cell membrane. No basement membrane is present. The other epithelial sheet (the supraradular epithelium) consists of cuboidal or low columnar cells, with more or less central, round nuclei (Fig. 51). These cells also contain rich basophilic granules and apparently give rise to the serrated dentins. Carriker and Bilstad (1946) described syncytium formation of these cells in *Lymnaea,* but the cell boundaries of the supraradular epithelium in *Australorbis* are clearly apparent.

The core or center of the radular sac is filled with a special type of supportive tissue, the collostyle (Fig. 50). Baecker (1932) described this particular tissue in *Helix* as "*Gallertgewebe*" and Carriker and Bilstad (1946) refer to it in *Lymnaea* as a gelatinous-like supportive tissue. The cells of the collostyle are irregular in shape and size, being round, ovoid, elongated or spindle-shaped and measuring 10 x 4 microns to 64 x 24 microns. They are packed together like epithelial cells. The nuclei are relatively small, round or oval, and poor in chromatin. The cytoplasm is lightly acidophilic and homogeneous but may contain filamentous material at times. Little PAS-positive material was demonstrated in these cells, but they stain weakly with alcian blue 8 GS. Muscle fibers of the radular retractor join the collostyle at the "opening" of the horseshoe (Fig. 50).

*Radular carrier.* The radular carrier is frequently referred to as the odontophoral cartilage and is composed of three elements bound together by connective tissue to form the shape of a boat; the floor of the boat is on the dorsal side to support the radular ribbon. The three pieces of tissue also form an enclosed sac which is connected to the circulatory system by a large blood vessel (Fig. 53). Since the radular carrier appears to have a pumping action,

and since an accessory heart has been reported in other molluscs (Michelson, 1956), the relationship of the lumen of the radular carrier with the circulatory system in *A. glabratus* suggests the possibility that it serves as an accessory heart in addition to possessing a supportive function. Histologically, the radular carrier is composed of vesicular cells and muscle fibers. The muscle fibers are the same type as those in the wall of the buccal mass, and run vertically to the surface of the radular carrier. The vesicular cells are polygonal, measure 70 x 30 microns and usually have relatively small nuclei (7 microns) which are eccentric and poor in chromatin (Figs. 18, 52). The cytoplasm is enclosed in a conspicuous cell membrane and contains a network of fine acidophilic filaments and some amorphous material. Both the fibrillar network and the cloudy material are strongly stained with PAS technic. Binucleated cells are sometimes seen. The vesicular cells in the antero-dorsal wall of the buccal mass are smaller than those in the radular carrier, but otherwise are similar. Both the inner and outer surfaces of the radular carrier are covered with thin connective tissue sheaths (Fig. 52).

The nature of the vesicular cells and their functions have been discussed by Baecker (1932) and are thought to be primitive cartilage cells (the prototypes of chondrocytes) and to serve as an elastic cushion for the radular ribbon.

*Esophagus.* The esophagus originates at the dorso-posterior wall of the buccal mass and runs posteriorly, parallel to and along the right side of the genital tracts. It joins the crop in the vicinity of the albumen gland. The ciliated simple epithelium is arranged in several longitudinal folds (Fig. 54). These folds clearly differentiate the esophagus from the postintestine where the folds are circular (Fig. 60). The epithelium consists of tall, uniform columnar cells (33 microns in a snail of 14.8 x 5 mm.) throughout the entire length of the esophagus (Fig. 55). They contain basal oval nuclei which are very rich in chromatin. The cytoplasm is filled with basophilic granules and may contain several vacuoles. The external surface is covered with long dense cilia (6 microns). Mucous cells or goblet cells are usually not found among the epithelial cells but do occur beneath the basement membrane in the muscle layers. The goblet cells measure 10 microns at the largest diameter, are tear-drop in shape and

contain relatively large nuclei (6 microns), rich in chromatin. In hematoxylin-eosin preparations these cells are difficult to recognize, but they stand out conspicuously in PAS-stained preparations. The goblet cells are morphologically distinct from buccal gland cells in that the former are smaller in size, are embedded singly among the muscle fibers and the cytoplasm is not basophilic. They secrete PAS-positive materials through the intercellular spaces of the epithelial lining.

Beneath the thick basement membrane are two layers of smooth muscle fibers; an inner longitudinal, and an outer circular layer. The muscle layers of the esophagus are thicker than those of the intestine. The longitudinal layer is thicker than the circular layer toward the buccal mass, but this characteristic is reversed near the crop.

*Stomach.* Baker (1945) recognized three anatomically distinct parts in the stomach of planorbids: 1) the crop, 2) the gizzard and 3) the pylorus.

Histologically, the crop and pylorus are similar. The simple epithelium of the two parts is composed of columnar cells (25 microns in an 18 x 5.5 mm. snail) and many goblet cells (Fig. 56). The chromatin-rich nuclei are oval and subbasal in position. The cytology of the epithelial cells does not differ materially from that of the esophagus except in size; the region also has many more goblet cells. Between the thin basement membrane and the outermost connective tissue sheath, there is a type of supportive tissue which does not resemble any other connective or supportive tissue observed in this snail (Fig. 56). It may attain 700 microns in thickness (18 x 5.5 mm. snail), but varies depending on the degree of distention of the organ. It resembles poorly differentiated mesenchymatous tissue with scarce cellular elements but is rich in collagenous-like fibers and ground substance. Two types of cellular elements are present in addition to smooth muscle fibers and amoebocytes. One of the cellular elements resembles a fibroblast and is more or less concentrated near the basement membrane. The other consists of irregularly shaped cells which vary considerably in size (4-18 microns). The nuclei of the latter cells are round or oval, usually eccentric in position and generally very poor in chromatic material. In hematoxylin-eosin preparations, the cytoplasm may appear vacuolated and

contain a few lightly acidophilic granules and brown pigment. The cell is, for the most part, obscure and difficult to recognize without special staining technics. The cell membrane stains green in Gomori's trichrome, appearing to enclose a vacuolated cytoplasm containing a nucleus. The vacuoles are filled with PAS-positive material in the form of granules or droplets. The ground substance is lightly basophilic, homogeneous and stains lightly with PAS technic. Collagenous-like fibers are lightly refractile and poorly stained in hematoxylin-eosin preparations but take a deep blue in Azan stain.

The smooth muscle fibers are not layered as in the intestine or esophagus, but run in various directions embedded in the ground substance of the supportive tissue.

The gizzard has the thickest muscular wall of the entire digestive tract and contains at least 10 layers at its middle portion. The inner surface is covered with simple columnar epithelial cells which measure up to 25 microns (18 x 5.5 mm. snail) and contain subbasal, oval nuclei. Except for the cuticular layer on the lumen surface of the epithelial cells of the gizzard these cells resemble those of the crop and esophagus. However, no mucus-secreting goblet cells were observed in the walls of the gizzard. Circular, longitudinal, oblique and radial muscle layers alternate in the wall, and weave a conspicuous pattern characteristic of the gizzard (Fig. 57). Cuticular epithelial cells have been observed in *Lymnaea stagnalis* (Carriker and Bilstad, 1946) and in *Helix* (Baecker, 1932) in the stomach. Many sand grains are usually present in the gizzard. Thus, the gizzard appears to serve primarily as a mechanical grinder of ingested foods.

*Intestine.* Baecker (1932) subdivided the intestine of *Helix* into *Duodenum, Blindsack* and *Enddarm.* We prefer, however, to subdivide the intestine of *A. glabratus* after the scheme used by Carriker and Bilstad (1946) for *Lymnaea stagnalis*, i.e., prointestine, midintestine, postintestine and cecum.

*Prointestine.* The prointestine makes a circular loop around the stomach after leaving the pylorus and is gradually transformed into the midintestine at the right side of the stomach. The epithelial sheet is most conspicuous in this portion of the intestine, occupies more than three-quarters of the intestinal wall, and displays an active secretory function. The epithelial

cells form a pseudostratified epithelium which may reach 88 microns in thickness in a snail of 18 x 5.5 mm. The nuclei are oval, are rich in chromatin, and lie at several levels (Fig. 57). The cytoplasm of some of these epithelial cells is filled with numerous basophilic granules, but in the majority it appears alveolar, the spaces being filled with a cloudy substance. Since this substance is strongly PAS-positive and is constantly discharged into the lumen of the intestine, it is likely that the prointestine is a secretory zone and corresponds to the glandular portion of the intestine of *A. glabratus* described by Marcuzzi (1950). The free surface of the epithelial cells is covered with dense short cilia (Fig. 58). The basement membrane is thin and difficult to discern. The muscular layers are also very thin and are composed almost entirely of circular fibers. The connective tissue sheath is relatively thick and consists of two to three layers of fibroblasts which may contain a few brown to brownish-black pigment granules.

*Midintestine.* The midintestine, beyond the prointestine, runs posteriorly along the dorsal side among the liver lobules, makes a "U" turn in the anterior third of the liver and continues anteriorly on the ventral side to become the postintestine near the pericardial sac. The intestinal wall is thinner in this portion than in any other area of the intestine including the esophagus. The epithelium is composed of the same type of ciliated columnar cells (18 microns in 18 x 5.5 mm. snail) as in the pylorus; however, there are more goblet cells (Fig. 59). There is no folding of this simple epithelium. The inner longitudinal muscle layer, almost absent in the wall of the prointestine, becomes more prominent in this portion.

*Postintestine.* The postintestine originates in the vicinity of the pericardial sac and is distinguished from the latter by circular folds which are formed by the epithelial sheet. It then enters the loose vascular connective tissue at the base of the central ridge (rectal ridge) and passes forward to the anus at the left rim of the pneumostome. The circular folds are conspicuous in longitudinal section and readily differentiate the postintestine from other portions of the digestive tract (Fig. 60). The columnar epithelial cells are taller than those of the midintestine and measure 42 microns in a snail of 18 x 5.5 mm.

(Fig. 61). The epithelial cells are similar in morphology to those found in the esophagus and the midintestine, but the mucus-secreting goblet cells are fewer than in the midintestine. The muscle layers shift their relative position as compared to the midintestine, so that the inner layer becomes circular and the outer layer longitudinal. Toward the anus (Fig. 62), the circular muscle fibers increase in number and form the anal sphincter. The basement membrane around the anus thickens considerably and contains much fibrillar material; some of the fibrils appear to run into the basal zone of the epithelial cells.

*Cecum.* The blind sac or cecum opens into the prointestine at its junction with the pylorus and shares a common opening with the hepatic duct. There are two low, opposing, longitudinal folds which, as in *Lymnaea stagnalis* (Carriker and Bilstad, 1946), delimit the incurrent and the excurrent tubules within the cecum. In addition to these folds the epithelial cells also form many fold-like circular elevations similar to those of the hepatic duct. Those cells covering the wall of the incurrent tubule, which is on the side of the hepatic duct, resemble the epithelial cells of the hepatic duct and possess a few goblet cells which secrete PAS-positive material. Those cells covering the excurrent tubule resemble the epithelial cells of the prointestine and actively secrete PAS-positive material (Fig. 63). Muscle fibers are scarce, but outer circular and inner longitudinal fibers are present. No basement membrane was observed. A thin connective tissue sheath covers the outer surface of the blind sac.

*Buccal gland.* Carriker and Bilstad (1946) studying *Lymnaea stagnalis,* claimed to have described the buccal gland for the first time. In *Helix pomatia,* this gland was called Nalepa's gland by Pacaut and Vigier (1906); however, since the cytology of the secretory cells could not be differentiated from that of the secretory cells of the salivary gland proper, Meisenheimer (1912) included it as part of the salivary gland. This group of gland cells in *Australorbis* is histologically distinct from the secretory cells of the salivary gland and should be identified as the buccal gland.

The major portion of this gland is located on the dorsal wall of the buccal mass, but extends to its ventral wall, as well as to a small portion of the esophagus. In fresh specimens the gland gives a characteristic yellow color to this area. The buccal gland

is composed of numerous mucus-secreting cells which form many small islands embedded among the muscular bundles of the buccal mass wall (Fig. 64). It is a ductless gland; the contractions of the surrounding muscle bundles apparently force the secretions through the intercellular spaces into the oral cavity. The individual secretory cells are usually pleomorphic but frequently they are flask-shaped. Large cells measure 15 microns at the base (in a snail of 18 x 5.5 mm.) when they are filled with PAS-positive material. The nuclei are round or slightly oval with chromatin practically filling the entire nucleus. The cytoplasm is strongly basophilic and also shows a positive reaction to PAS. However, it does not show metachromasia with toluidine blue or thionin. The buccal gland cells are similar to mucous gland cells in the foot and cannot be differentiated from the latter.

*Salivary gland.* The salivary gland of *A. glabratus* is a paired tubular organ, the distal ends of which are joined, thus forming a loop on the dorsal wall of the esophagus at its middle third. Each gland has a short duct which opens to the buccal cavity on the lateral aspect of the esophagus. The gland does not have an acinar structure as it does in *Lymnaea stagnalis* (Carriker and Bilstad, 1946), but the tubular wall bulges slightly to form haustra-like folds which resemble those of the vertebrate colon. No basement membrane was demonstrated in the epithelial sheet with the staining methods used. The epithelium rests on a thin connective tissue sheath which contains some dark brown pigment. Sub-epithelial smooth muscle fibers were described in *Helix* by Baecker (1932), but we did not observe them in *A. glabratus*. The ducts are short and lined with cuboidal, non-secretory epithelial cells that have long cilia on the surface. The nuclei are usually round, rich in chromatin granules and situated centrally. The cytoplasm is filled with acidophilic granules and may also contain a few vacuoles. The secretory cells gradually appear among the duct epithelial cells lying between the non-secretory cells in the basal zone. These secretory cells gradually increase in size and number toward the gland proper; they compress the duct epithelial cells and become the principal cell (Fig. 65). The flattened duct epithelial cells of the gland proper are very slender and are hardly recognizable

among the secretory cells except for their acidophilic, thread-like cytoplasm with a centrally located basophilic nuclear outline. The epithelial cells of the duct retain the long cilia and probably function as supportive structures for the secretory cells as well as propelling secreted materials (saliva) to the buccal cavity by the movement of the cilia. Pacaut and Vigier (1906), studying *Helix,* and Carriker and Bilstad (1946) studying *Lymnaea stagnalis,* differentiated several secretory stages in the secretory cells, but it was difficult to differentiate comparable stages in *Australorbis.* The actively secreting cells are tall columnar and measure 50 microns in height with round nuclei of 15 microns in an 18 x 6.0 mm. snail (Fig. 66). The nucleus is extremely rich in coarse chromatin, usually contains a large nucleolus and resembles the nucleus of a ganglion cell. Since cell function and regeneration are not synchronous, cells of various sizes are usually seen in a given area. The nuclei also are not of equal size and are located on two or three levels, *i.e.,* basal, central or subperipheral (Fig. 66). The cytoplasm is filled with a fine, basophilic reticular net which holds large amounts of secretory materials in droplets or coarse granules. These materials sometimes show light acidophilia, sometimes remain unstained in hematoxylin-eosin preparations, but are usually stained by PAS which frequently reacts strongly and masks the basophilic reticular net. Active secretion of the glandular cells apparently occurs by rupture of the cell membrane and thus the cell contents are discharged into the lumen of the gland (Fig. 66). Since degenerated nuclei of glandular cells frequently occur among the cell debris in the lumen, the secretory cells probably disintegrate completely after secretion (holocrine). Young secretory cells differentiate from fibroblasts in the connective tissue sheath. The cytoplasm of the differentiating fibroblast first thickens and becomes pyramidal, with the base of the cell resting on the connective tissue sheath. These young cells gradually grow larger and assume the morphology of columnar secretory cells with round, chromatin-rich nuclei; the cytoplasm accumulates a basophilic reticular net as well as PAS-positive material during the process.

*Liver.* The liver is a massive digestive gland and occupies the caudal two-thirds of the snail body together with the ovotestis; the latter is approximately one-fifth of the size of the liver. The liver is a compound tubular gland, consisting of a main hepatic duct with one short dorsal branch and numerous secretory lobules (Figs. 1, 5, 68). The main duct runs anteriorly along the ventral side of the lobules, passes into the cecum and thence via a common opening into the prointestine at its junction with the pylorus. The short, dorsal branch unites with the main duct shortly before its point of union with the cecum (Fig. 5). The simple columnar epithelium of the hepatic duct is raised in numerous fold-like, circular elevations which, in cross section, are dome-shaped, finger-shaped or fungoid in appearance (Fig. 67). These elevations decrease posteriorly in number and height and the epithelial sheet finally becomes smooth. The elevations are caused by different sizes of epithelial cells. Those in the elevated areas measure 25 microns in height and elsewhere measure 14 microns (in an 18 x 5.5 mm. snail). The epithelium of the raised areas near the opening of the duct into the cecum has a pseudostratified structure, but this is lost as the epithelium passes posteriorly. The free surface of the cells is covered with cilia. The cilia of each cell arise from a point near the nucleus, radiate to the surface, and penetrate through the basal bodies before becoming free in the lumen. This type of structure for ciliary apparatus has been observed in *Helix* by Baecker (1932). Mucus-secreting goblet cells are also present among the ciliated columnar cells. Except for the basal bodies of the cilia, the cytology of the epithelial cells of the hepatic duct is similar to that of the epithelium of the pylorus. Mitotic figures are occasionally seen in the epithelium of the hepatic duct. No basement membrane is recognized, and the epithelium is covered with a thin, connective tissue sheath which contains a few collagenous-like fibers. A few delicate smooth muscle fibers, mostly longitudinal, are seen between the connective tissue sheath and the epithelial sheet near the opening. The lobules of the liver are also covered with a thin, connective tissue sheath which is continuous with that of the hepatic duct. No basement membrane was observed in the lobules. Each lobule is embedded in and separated from its neighbor by a loose vascular connective tissue

which is continuous with that of the ovotestis. Numerous blood spaces, with varying numbers of vesicular cells and pigment cells, are present in the interstices of the connective tissue. The vesicular cells are similar to those described for the radular carrier and are perhaps storage-cells for polysaccharides. Von Brand and Files (1947) described storage of glycogen in the liver and ovotestis of *Australorbis glabratus* but did not specify where.

Faust (1920), Baecker (1932), and Carriker and Bilstad (1946) agree that only two types of cells (lime cells and digestive cells) occur in the liver lobules of the snails studied. In *Australorbis*, mucus-secreting goblet cells are present in addition to the digestive cells and lime cells. The goblet cells are sparsely scattered among the other two types of cells and cannot be differentiated from the young digestive cells except when PAS stain is used. They take a deep stain with leucofuchsin and are morphologically similar to those present in the other parts of the digestive tract. The lime cells are more abundant than the goblet cells and are usually pyramidal or rhomboidal in shape with their bases lying on the connective tissue sheath (Fig. 70). The larger cells measure 40 microns across (20 x 6.4 mm. snail) with relatively large, round nuclei (measuring 12 microns) which are extremely rich in chromatin granules and usually contain a large nucleolus. The cytoplasm is filled with basophilic granules and fibrillar reticulum; it may also include vacuoles of various sizes, but not inclusion bodies or the yellow excretory bodies of the type noted in the cytoplasm of the digestive cells (Fig. 68). The lime cells are embedded between digestive cells and usually do not reach the lumen surface except after breakdown of the latter in the secretory process. It has been observed that after the surface cell membrane ruptures, the nuclei may lose chromatin granules and separate from the cytoplasm. Therefore, it would appear that the secretory processes of the lime cells are holocrine in nature.

The digestive cells constitute the principal glandular epithelial cells and show considerable polymorphism. Krijgsman (1925) described four stages in the digestive cells of *Helix pomatia* and classified their secretory function as being apocrine in nature. Similarly four physiologic stages could be recognized

in the functioning of digestive cells of *Australorbis*. The digestive cells appear to break down completely during secretion (holocrine), and new cells arise or are differentiated from cells of the connective tissue sheath. The fibroblasts are first transformed into columnar cells which resemble the epithelial cells of the hepatic duct except that there are no cilia. The nuclei become round, are located subbasally and are rich in chromatin granules (Fig. 69). The cytoplasm is filled with basophilic granules and a reticular net. No inclusion bodies appear at this stage, and the lumen surface of the lobule is smooth (Fig. 69). In the second stage, the cytoplasm begins to accumulate secretory materials in the peripheral zone which is filled with coarse acidophilic granules (Fig. 59). Owing to the uneven accumulation of these acidophilic granules, the lumen surface of the lobule becomes irregular and cells become pleomorphic. In the third stage, vacuoles of various sizes appear in the cytoplasm peripheral to the nuclei which are now forced to a basal position (Figs. 68, 70). Yellow globular inclusion bodies, or so-called excretory bodies, are frequently found in the vacuoles, at first very small and several in number but later becoming larger in size and fewer in number. They are not stained in H-E preparations, assume their own yellow color, are lightly positive to PAS, and may also be stained with fast green (*gruene Granula* of Krijgsman, 1925 and 1929). The digestive cells reach their peak of growth at the third stage and measure 70 microns in height (20 x 6.4 mm. snail). At the fourth stage the cell membrane on the lumen surface ruptures, and the cell discharges its contents. The nuclei lose their rich chromatin granules, float free in the empty cells and finally disappear. The cytoplasm near the nucleus retains its basophilia until nearly replaced by vacuoles just prior to cell dissolution. The lumen of the lobules at the beginning of secretion is filled with cellular debris which transforms into an amorphous cloudy mass. This cloudy mass is lightly acidophilic and also stains lightly with PAS. Although the liver is directly connected with the intestinal tract, bacteria and other microorganisms are seldom seen in the hepatic lumen. Fedele (Baecker, 1932) studying "Opisthobranchium," ascribed secretory, phagocytic, absorptive and excretory functions to the

liver cells. We were able to obtain evidence only of secretory and possibly excretory functions in the cells of liver lobules in *A. glabratus*.

## IX. Reproductive System

Since pulmonate snails may be identified by the characters of the reproductive system, the anatomy and histology of the reproductive organs have been studied heretofore in greater detail than those of the other systems (Baker, 1945; Hubendick, 1955). The anatomical descriptions of the reproductive organs of *A. glabratus* by Baker (1945) and Paraense and Deslandes (1955) are essentially similar except that the latter authors recognized the common collecting canal of the ovotestis as histologically different from the diverticula and hermaphroditic duct.

The genital system of *A. glabratus* can be subdivided into a) the common genital organs (hermaphroditic organs), b) male genitalia and c) female genitalia.

*Common genital (hermaphroditic) organs.* The common genital organs consist of a highly-branched ovotestis with its collecting canal and a hermaphroditic duct. The acini of the ovotestis are histologically and functionally distinct from the collecting canal. In spite of the morphological differences, Baker (1945) apparently regarded this collecting canal as part of the hermaphroditic duct. The cephalic or anterior portion of the collecting canal is expanded to form a pouch-like structure which abruptly narrows at its end to join the seminal vesicle or the origin of the hermaphroditic duct by a thin, "S"-shaped tube (Fig. 75). The hermaphroditic duct conveys mature male and female sexual cells into the vas efferens (sperm duct) and carrefour respectively.

*Ovotestis.* The walls of the acini of the ovotestis are composed of thin connective tissue, two to three cells thick, with abundant collagenous-like fibers. This wall, "Ancel's layer" (Ancel, 1902), contains cells which, in section, are morphologically similar to fibroblasts. Although Abdel-Malek (1954 a, b) in *Helisoma* and *Biomphalaria* and Merton (1930) in *Planorbis* described germinal epithelium with a basement membrane in the ovotestis, we observed no such specially differentiated layer in *Australorbis*.

It appears, however, that the germinal cells differentiate from the innermost cells of Ancel's layer by a thickening and transformation of the cytoplasm and nucleus. In section, the female germinal cells or ova are usually located at the apices of the acini, and the male germinal cells are arranged along the side walls (Fig. 71). The very early stages (spermatogonia) of the male germinal cells are frequently located near the atrium of an acinus. The maturing stages of the male cells generally line the wall of the acinus from the atrium toward the apex (Fig. 71), and the maturing spermatozoa attaching to the basal or Sertoli cells are close to the area where the ova are developing. The developing young male germinal cells are attached to Sertoli cells by cytoplasmic stalks, which in section frequently are not apparent, and thus some of the germinal cells appear to be free in the lumen (Fig. 90). The youngest male germinal cells are tear-drop in shape and measure 6 microns at the base. The chromatin-rich nuclei fill more than two-thirds of the cytoplasm which is also extremely rich in basophilic material. The spermatogonia separate by mitotic division to form spermatocytes which enlarge considerably before undergoing another division. The cytoplasm of the spermatocytes gradually loses its basophilia and becomes slightly acidophilic. Another mitotic division takes place (Fig. 72) resulting in the formation of spermatids. The spermatids are about the size of spermatogonia and half the size of the spermatocytes. The small round nuclei of the spermatids are at first compact, but before the transformation into spermatozoa is complete the chromatin material becomes concentrated and crescent-shaped (Fig. 89). The nucleus finally becomes helicoid, and the cytoplasm gives rise to an acidophilic tail portion or flagellum by elongation (Figs. 89, 90). Although meiosis must take place in the process of spermatogenesis, no special study was made of the reduction divisions in *A. glabratus*. The mature spermatozoon (Fig. 96) has a slightly flattened cephalic portion, shaped like a corkscrew, and a long flagellum with two loosely-wound spiral coils encircling the axis cylinder.

The Sertoli cells also differentiate from Ancel's layer at an early stage of spermatogenesis, but they remain inconspicuous until the spermatogonia reach the spermatid stage. The Sertoli cells vary in size and shape considerably, appearing as half-moon

or columnar-shaped. They contain one or occasionally two oval nuclei which are rich in chromatin, and contain a large nucleolus. A wedge-shaped constriction may occasionally be seen in the nucleus of Sertoli cells (Fig. 89). The cytoplasm is filled with a fine reticulum which may be acidophilic or basophilic. Vacuoles in varying number may be present in the Sertoli cells.

The female germinal cells are nearly always located at the apex of each acinus in small numbers, and also differentiate from the cells in Ancel's layer (Fig. 73). The mature ovum measures 98 microns in diameter and contains a round, slightly eccentric nucleus measuring 36 microns. The nucleolus is round, eccentric, and has a basophilic, half moon-shaped paranucleolus along the margin. The cytoplasm stains purple or bluish-purple in hematoxylin-eosin preparations, is coarsely granular, and may also contain a few small vacuoles. PAS-positive material may be present at times, as reported by von Brand and Files (1947). The nurse cells, which are equivalent to the Sertolis of the male germinal cells, adhere to the ovum to form an enveloping sac. A follicular cavity may occur between the nurse cells and ovum. Abdel-Malek (1954 a) described the presence of a follicular cavity in *Helisoma trivolvis*. Degenerating female germinal cells are frequently seen among the maturing ova.

*Collecting canal.* The collecting canal of the ovotestis is lined with a sheet of cuboidal cells which may have the appearance of transitional epithelium when the canal is not distended. No basement membrane is present, and the epithelial sheet is directly covered with a connective tissue sheath rich in collagenous-like fibers. A few delicate, smooth muscle fibers are present beneath the epithelium. The collecting canal is capable of great distention to accommodate the large numbers of germinal cells (mostly spermatozoa) produced at certain stages of reproduction. When the canal is distended, the epithelial cells become almost flat with the compressed nuclei occupying a central position. The epithelial sheet forms several longitudinal folds when the canal is not distended. The epithelial cells are then compressed and appear wedge-shaped with dome-like surfaces forming irregular wavy outlines in the lumen, and the oval nuclei are irregularly located at several levels, thus giving the epithelial sheet a transitional appearance (Fig. 74). Short cilia may be seen on these

cells. PAS-positive material can be demonstrated in the cytoplasm peripheral to the nucleus. The acidophilic cytoplasm is usually finely granular, containing a delicate reticulum.

*Hermaphroditic duct or ovisperm duct.* The hermaphroditic duct in *Australorbis* is histologically distinct from the collecting canal of the ovotestis and is not capable of great distention (Fig. 77). The duct joins the collecting canal via a small-calibre, "S"-shaped tubule (Fig. 75). Beyond this junction the hermaphroditic duct enlarges and possesses many diverticula which are usually filled with mature spermatozoa. This portion of the duct is generally called the seminal vesicle (Baker, 1945) (Fig. 76). The lumen of the duct, as well as the diverticula, is lined with simple cuboidal epithelium with central, round nuclei rich in chromatin. The epithelial cells in various diverticula may vary slightly in size. Contrary to the report of Paraense and Deslandes (1955), we have found the free surface of the epithelial cells to be covered with short, dense cilia. The cytoplasm is filled with lightly basophilic granules and may also contain vacuoles. Abdel-Malek (1954 a) described a syncytial form of the diverticular epithelium in *Helisoma*, but this character was not observed in *Australorbis*. The cytoplasmic boundary is particularly clear in preparations stained with Azan or Gomori's trichrome. Cilia are present throughout the entire duct. Beyond the seminal vesicle, the duct gradually narrows and becomes very small before joining the carrefour. Smooth muscle fibers are present beneath the epithelial sheet. A thin connective tissue sheath covers the outer surface. The duct joins the carrefour tangentially so that part of its wall is elevated from the surface of the carrefour (Fig. 97).

*Male genitalia. Sperm duct or vas efferens.* The male genitalia consist of the prostatic gland and genital tract. The genital tract is subdivided into sperm duct (vas efferens), vas deferens, and penial complex (Baker, 1945; Paraense and Deslandes, 1955). The prostatic gland is formed by evaginations of the sperm duct and possesses the same histological structure as the duct. Although the sperm duct in *Australorbis* is very important in the reproductive process of this hermaphroditic snail, the precise origin of the duct has not been described. This is probably due to the extremely small calibre of the duct at its origin, thus

making the exact location of its departure from the hermaphroditic duct difficult to find by gross dissection. Abdel-Malek (1954 a) showed that the sperm duct of *Helisoma* arises from the hermaphroditic duct just before the latter empties into the carrefour. The sperm duct in *Australorbis* originates from the hermaphroditic duct at its opening into the carrefour; thus both ducts in reality have a common opening into the carrefour. For a distance of approximately 200 microns from its origin, the sperm duct is about 33 microns across and is histologically distinct from the rest of the duct. The epithelium of this portion consists of low cuboidal, non-secretory cells covered with long, dense cilia (Fig. 78 a). The cytoplasm is acidophilic, and the nucleus is compact. The epithelial sheet is invested with many smooth muscle fibers, most of which are circular and constitute the inner layer. The muscle layers are covered with connective tissue which is common to the carrefour, the end portion of the hermaphroditic duct and the first portion of the oviduct. Continuing toward the penial complex, the epithelial cells of the sperm duct gradually increase in height to become columnar, and secretory cells appear among the non-secretory (Fig. 78 b). The secretory cells finally predominate and compress the non-secretory cells which become small and obscure (Fig. 81). Both types of cells alternate in the epithelial sheet. The secretory cells measure 52 microns (20.0 x 6.4 mm. snail), and have round to oval, chromatin-rich nuclei (7 microns) located in the basal zone (Fig. 81). The cytoplasm in actively secreting cells contains a basophilic reticulum, the meshes of which are filled with secretory droplets. These droplets appear first as fine granules but later coalesce and become droplets or globules. In hematoxylin-eosin preparations, the secretory granules stain blue or blue-purple, and the droplets stain pale blue or are refractory to staining. In PAS technic, the secretory granules stain weakly, and the droplets stain strongly. The non-secretory cells are as tall as the secretory and are ciliated. The cytoplasm is usually so compressed between the secretory cells that it appears as an acidophilic thread. The central nuclei are then so small and compact that only a blue oval outline can be distinguished. The epithelial sheet is invested with a few delicate circular, smooth muscle

fibers but is without a basement membrane. A thin connective tissue sheath containing some dark brown pigment covers the outer surface.

*Prostatic gland.* The prostatic gland is histologically similar to the glandular portion of the sperm duct and represents evaginations of the latter.

*The vas deferens.* The sperm duct tapers abruptly in the vicinity of the duct of the seminal receptacle and is transformed into the non-secretory vas deferens (Fig. 82). The vas deferens continues toward the praeputium, enters the tissue of the neck near the male genital opening and makes a "U" turn on the dorsal surface of the praeputium; then lies free in the coelomic cavity and joins the verge. Histologically, the portion of the vas deferens between the sperm duct and the "U" turn (proximal leg) is different from the portion between the "U" turn and the verge (distal leg). The columnar epithelial cells of the sperm duct are replaced abruptly by densely ciliated, non-secretory, cuboidal cells which rest on a thick basement membrane. The nuclei of the cuboidal cells are round, central in position and rich in chromatin granules. Circular muscle fibers which are sparse in the sperm duct become abundant. Longitudinal fibers do not appear in the outer layer until the proximal leg reaches the "U" turn. The proximal leg is narrower (66 microns at its origin and 33 microns near the "U" turn in a snail of 20 x 6.4 mm.), is usually oval in cross section, and contains few longitudinal muscle fibers (Fig. 83). The distal leg is thicker (uniformly 122 microns in a snail of 20 x 6.4 mm.), round in cross section, and the outer longitudinal muscle layer is as thick as the inner circular layer (Fig. 84). The muscle fibers of the distal leg, especially the longitudinal fibers, contain a large amount of PAS-positive material around the nuclei, and then appear vacuolated in cross section in hematoxylin-eosin preparations (Fig. 84). A thin connective tissue sheath covers the outer surface of the vas deferens.

*Penial complex.* The penial complex is composed of the verge, the vergic sac and the praeputium (Baker, 1945). The inner surface of the verge is lined with a layer of low cuboidal cells containing ovoid, central nuclei and bearing dense, long cilia.

The epithelial cells rest on a basement membrane which is almost as thick as the epithelial sheet. Beneath the basement membrane are two layers of muscle fibers, an inner circular and an outer longitudinal. A thin connective tissue sheath covers the outer surface (Fig. 85 a).

The vergic sac is lined with a sheet of nonciliated cuboidal cells. The basement membrane is invested with a layer of inner circular and outer longitudinal smooth muscle fibers. The outer surface of the vergic sac is covered with a relatively thick connective tissue sheath containing rich dark brown pigment. The sac is frequently seen in an invaginated position in the fixed specimen (Fig. 85 b).

The praeputium opens on the neck behind the base of the left tentacle and is characterized by a highly-developed muscular wall, especially in the region of the two opposing longitudinal ridges called pilasters (Fig. 86). The pilasters extend into the lumen which appears "H"-shaped in cross section. The simple epithelium consists of columnar cells with dense, long cilia. The nuclei are very rich in chromatin, ovoid in shape and subbasal in position. A thick basement membrane supports the epithelial sheet. Two layers of circular muscle fibers are present, one in contact with the basement membrane and the other in contact with the connective tissue sheath covering the outer surface. Between these two layers, there is a zone of connective tissue which is richly invested with both longitudinal and radial muscle fibers. The longitudinal fibers are separated into bundles by radial fibers and connective tissue (Fig. 86). The longitudinal bundles are especially well-developed in the pilasters. No mucous cells are present in the epithelial sheet, but they occur in the connective tissue, apparently discharging their secretions into the lumen via the intercellular spaces of the epithelial cells. Abundant small pigment cells are found in the connective tissue sheath and among the muscle fibers.

The region between the praeputium and the vergic sac is called the diaphragm (Baker, 1945). This is a muscular ring with papilla-like protrusions of epithelial folds into the lumen (Fig. 87). The epithelial cells are low columnar, bearing a cuticular covering on the surface and have round chromatin-rich

nuclei in the subbasal zone. An inner layer of circular and an outer layer of longitudinal muscle fibers lie beneath the basement membrane.

*Female genitalia.* The female genitalia include the albumen gland, carrefour, oviduct, nidamental gland, uterus, spermatheca (seminal receptacle) and vagina (Baker, 1945). The carrefour, oviduct, nidamental gland, uterus and vagina comprise a continuous duct which carries the mature ova to the exterior. The microscopic anatomy of the female genitalia follows a general scheme like that previously described in *Lymnaea stagnalis* by Holm (1946). The simple epithelial sheet contains two types of cells, a massive secretory and a slender supportive cell. These two cells alternate quite regularly to form the duct lining. There is usually no basement membrane beneath the epithelium. Delicate smooth muscle fibers are seen between the epithelium and the outer connective tissue sheath.

*Albumen gland.* This is a compound tubular gland situated on the dorsal side of the stomach. Two histologically distinct structures are present: a main excretory duct and a large number of highly branched secretory tubules. The main excretory duct opens into one pole of the carrefour which histologically is an enlarged end portion of the duct (Fig. 79). The simple epithelium of the duct consists of low columnar cells covered with long dense cilia. The cytoplasm contains acidophilic striations running vertically to the surface and a central, oval nucleus. The lumen is frequently filled with a cloudy, lightly basophilic secretion of the gland. No basement membrane was observed beneath the epithelium which is invested by inner longitudinal and outer circular smooth muscle layers. The connective tissue sheath covering the outer surface is continuous with that of the gland.

The epithelium of the secretory tubules contains two types of cells, a massive secretory and a slender supportive cell. The secretory cells vary considerably in size and structure depending on the phase of secretory activity. In a snail of 20 x 6.4 mm., they measure 12 x 7 microns as secretory globules begin to accumulate. The nuclei measure 5 microns, are round, central in position, extremely rich in chromatin, and contain a large nucleolus. The cells gradually enlarge and measure 30 x 22.5

microns just before the globules are discharged. The secretory materials appear first as fine granules embedded in an amphophilic (purple-red in H-E preparation), cytoplasmic reticulum (Fig. 88). They coalesce and form one or more large globules which are secreted into the lumen through the ruptured cytoplasmic membrane. The scanty cytoplasm which is forced to the basal region at this stage is highly basophilic and cannot be differentiated clearly from the darkly stained (pyknotic) nucleus. The globules stain a light blue in H-E preparations, blue in Azan, bluish-green in Gomori's trichrome, are strongly positive with PAS, but do not stain with thionin or toluidine blue O. The secretory materials in the lumen also react in a similar manner with these stains. Von Brand and Files (1947) reported that the galactogen was responsible for the PAS reaction in this gland. Millon's reaction was also applied with a moderately positive result. The supportive cells are usually compressed tightly between the massive secretory cells and show poorly defined cytology. The acidophilic cytoplasm appears as a thin thread containing an elongated blue nucleus in the center. The nuclei of the supportive cells may be displaced either toward the basal or the peripheral zone. In the latter case, they were described in land pulmonates by Cavalié and Beylot (1902) as "*Cellules centrotubuleuses,*" but in *Australorbis* are actually cells of a supporting nature, as described by Baecker (1932). The secretory tubules are covered by a thin connective tissue sheath. The tubules are separated by connective tissue containing small pigment cells and abundant blood spaces.

*Carrefour.* Baker (1945) called the bean-shaped swelling at the end of the albumen gland duct the "carrefour" (Fig. 97). It had earlier been described and considered to be the site of fertilization of the ova in hermaphroditic land pulmonates (Meisenheimer, 1907 and 1912). The hermaphroditic duct opens tangentially into the carrefour opposite the opening of the duct of the albumen gland. Macroscopically, it appears partially embedded in the wall of the carrefour. The oviduct opens on the side wall of the carrefour between the sperm duct and the duct of the albumen gland. Except that the epithelial sheet contains some mucous cells and is infolded, the structure of the carrefour cannot be distinguished from that of the duct of the albumen

gland and therefore, the carrefour should be regarded as the enlarged end portion of this duct (Figs. 79, 80). From its micro-anatomical and histological structures, it appears that the function of the carrefour in *Australorbis* is more likely a device for separating the male and female germinal cells into their respective genital tracts than a fertilization site as reported by Meisenheimer (1907) for *Helix pomatia*, and in *Helisoma* and *Biomphalaria* by Abdel-Malek (1954 a, b). Since this structure has not been described in dioecious snails, and since the sperm duct is extremely small in calibre at its opening to the carrefour and shares a common opening with the hermaphroditic duct, the spermatozoa are probably delivered to the sperm duct directly, while the ova, too large to enter the sperm duct, are passed to the carrefour to be delivered to the oviduct.

*Oviduct.* The oviduct originates from the carrefour, runs anteriorly in the coelomic cavity along the sperm duct and expands into the nidamental gland as a pouch-like swelling in the vicinity of the posterior end of the prostatic gland (Baker, 1945) (Fig. 97 e). The epithelial cells of the oviduct are differentiated from those of the carrefour by their glandular structure, basophilic staining, and the absence of dense cilia. The lumen of the duct is folded irregularly. The secretory cells are massive and columnar measuring 87 microns in height (15 x 5.1 mm. snail) and contain relatively small compact nuclei in the basal zone (Figs. 79, 80, 91). The cytoplasm is filled with a basophilic, fine reticulum, containing amorphous secretory material. The secretory material stains strongly with alcian blue and PAS, and shows metachromasia with thionin (beta metachromasia). These reactions indicate the presence of acid mucopolysaccharides. The non-secretory cells were called sustentacular cells by Paraense and Deslandes (1955), and are tightly compressed between the secretory cells. They are poorly differentiated and usually appear as light acidophilic threads containing thin, central, ellipsoidal nuclei. Contrary to Paraense and Deslandes (1955), we found the sustentacular cells to be sparsely covered with long cilia on the surface. Like those of the sperm duct, the cells are apparently supportive structures for the oviduct. No basement membrane was observed and the epithelial

sheet is invested directly with a few delicate smooth muscle fibers. A thin connective tissue sheath covers the outer surface.

*Nidamental gland.* The anterior end of the oviduct is enlarged considerably and is twisted into a half circle to form a pouch-like structure called the "nidamental gland" by Baker (1945) (Fig. 98). Its lumen is almost completely occluded by irregular epithelial folds. The secretory and sustentacular cells are the same size as those in the oviduct; however, the staining reactions of the secretory cells are strikingly different (Fig. 91). Over a small area facing the spermatheca the epithelial sheet contains only non-secretory, low columnar, acidophilic cells (about one-fourth of the height of secretory cells) possessing abundant cilia. These cells are also sustentacular in nature and are not modified by the pressure of the secretory cells. The slender sustentacular cells seen in the oviduct are also present among the secretory cells of the nidamental gland. The majority of the secretory cells are filled with acidophilic secretory globules which press the small, compact oval nuclei to the basal zone. These globules are strongly stained with PAS and show purple metachromasia with thionin (beta metachromasia) but are not stained by alcian blue, thus indicating a different chemical nature from the secretory substance in the oviduct. A small number of the secretory cells stain lightly basophilic in H-E preparations and lack secretory globules. Their cytoplasm is filled with cloudy material containing fine granules, which stain positively with PAS but show much weaker metachromasia with thionin than do the acidophilic cells. The cloudy material does not stain with alcian blue. The smooth muscle fibers are minimal in the wall covered by the secretory cells but are more abundant in the wall covered only by the low columnar sustentacular cells.

*Uterus.* The uterus is a short segment of the female genital tract that connects the nidamental gland to the vagina. It is not differentiated macroscopically from the nidamental gland except for its wider lumen. Histologically, differences are apparent in the epithelial sheet and in the muscle layer (Fig. 92). The secretory cells in the uterus resemble the basophilic secretory cells of the nidamental gland. At the area of transformation from the nidamental gland, the secretory cells are approximately the same size as those in the latter, but gradually become smaller

toward the vagina. The cytoplasm is reticular and contains basophilic secretory material. This material is PAS-positive but is negative with alcian blue and shows no metachromasia with thionin. The compact nuclei are oval and are located between the mid- and basal zones. The non-secretory sustentacular cells are more abundant and less tightly pressed between the secretory cells than those in the nidamental gland. These cells become very numerous and finally replace the secretory cells completely to transform into vaginal epithelium (Fig. 93). Cilia are abundant owing to the increasing number of sustentacular cells. The non-secretory area of the epithelium in the nidamental gland is continuous with the uterus and ends at the junction of the latter with the vagina. No basement membrane is present beneath the epithelium. The muscle fibers become more numerous toward the vagina and form inner longitudinal and outer circular layers. The outer connective tissue sheath contains small pigment and mucous cells.

*Vagina.* The vagina is the only segment in the female genital tract wherein the epithelial sheet rests on a basement membrane. The irregular epithelial folds of the uterus are rearranged into several longitudinal folds. The epithelial sheet is composed of non-secretory, heavily ciliated, columnar cells, among which occur a few mucus-secreting goblet cells. The cytoplasm is acidophilic, containing oval nuclei in the basal zone. The inner longitudinal muscle fibers become less abundant, while the outer circular fibers become very well developed toward the female genital opening. This aperture is located between the male genital opening and the anus. The lumen usually appears occluded by the long cilia and the epithelial folds. The outer connective tissue sheath is fused with the surrounding tissue of the neck and contains abundant small mucous cells (Fig. 95).

*Spermatheca or seminal receptacle.* The spermatheca is a pear-shaped sac which opens into the vagina at its middle and posterior thirds. The short duct of the spermatheca is similar histologically to the vagina. The heavily ciliated, simple columnar epithelium of the duct forms several longitudinal folds and rests on a relatively thick basement membrane (Fig. 94). The inner longitudinal and outer circular muscle layers beneath the basement membrane are well developed. The anterior half of the

duct is embedded in connective tissue in common with the vagina and a portion of the proximal leg of the vas deferens. The cilia of the epithelial cells are long and dense near the opening but become shorter and more sparse toward the sac epithelium and finally disappear on the latter. The longitudinal muscle fibers of the duct run into the spermatheca. The epithelium of the sac is composed of columnar cells which decrease in size from the duct to the end of the sac. Many folds are present when the sac is empty. The columnar cells become cuboidal when the sac is distended. The chromatin-rich nuclei are round and located in the basal zone. The cytoplasm is filled with a fine basophilic reticulum and may occasionally contain several small vacuoles (Fig. 85). The cytoplasm superficial to the nucleus stains with PAS but does not take up alcian blue or show metachromasia with thionin. The epithelial cells apparently possess secretory functions. The spermatozoa in the spermatheca may occasionally lose their structure completely and appear degenerate.

## SUMMARY AND CONCLUSION

A histological study of *Australorbis glabratus* has been carried out as a necessary requisite for subsequent histopathological investigations on this snail. The results are presented as a systematic description of nine organ systems or tissues. It is believed that this study represents one of the first of such descriptions of a fresh-water snail, although similar descriptions exist for the land pulmonates.

The epidermal tissue consists of simple epithelium except for a small area of the mantle collar where pseudostratified epithelium is present. The epithelia of the foot surface, the tentacles and a small portion of the mantle cavity are heavily ciliated.

Two types of connective tissue are recognized: a) the dense connective tissue containing abundant fibroblasts, pigment cells, collagenous-like fibers and ground substance but lacking conspicuous circulation spaces; b) the loose "vascular" connective tissue characterized by the presence of numerous circulation spaces formed by a meshwork of fibroblasts. The fibroblasts appear to be an important cellular element owing to their ability

to transform into amoebocytes under certain stimuli and to repair damaged tissue.

The muscular tissue contains three types of muscle fibers: a) the granular muscle fibers, confined to the heart; b) the intermediate granular muscle fibers found only in the buccal mass; c) the smooth muscle fibers composing the rest of the muscular tissue of the other organs. The structure of the heart muscle in *A. glabratus* differs from that of the land pulmonates which possess obliquely striated fibers.

Eleven ganglia forming a ring around the esophagus comprise the central nervous system. These ganglia are connected to one another by commissures. The ganglion cells are arranged peripherally, and the nerve fibers centrally, in each ganglion. The statocyst, which is imbedded in the epineurium at the dorsoposterior corner of each pedal ganglion, is lined with two types of epithelial cells and contains a number of ovoid statoliths. The eyes are well developed and structurally are composed of the optic capsule, cornea, retina, lens, vitreous humor and optic nerve. The osphradium is a pear-shaped sac enveloped at its base by the osphradial ganglion and is located at the junction between the mantle collar and the neck on the left side of the median line. This organ has not been described in land pulmonates and is believed to be a sense organ present only in aquatic snails. The tentacle has a dense connective tissue core containing a central artery, and has peripheral blood sinuses in the region between the core and the epithelial sheet. There are five groups of conspicuous peripheral sensory cells, one at the base of each tentacle and one at the margin of each lip.

The heart is provided with two valves, the atrioventricular and aortic valves. No endocardium was observed, but the epicardium is well defined. The only type of blood cell, the amoebocyte, is probably formed under normal conditions in lymphoid tissue located in the wall of the kidney, and in the blood sinuses. The lymphoid tissue has not been reported (in the pulmonate) prior to this study and in appearance resembles the medulla of a lymph node in the vertebrates.

The respiratory surface is covered with four types of epithelial cells: flat, cuboidal, columnar without cilia, and ciliated columnar. The last type of epithelial cells has not been reported in the land pulmonates.

Unlike *Helisoma* sp., the renal organ of *A. glabratus* consists of two distinct parts, an anterior tubular and a posterior saccular portion. The lumen of the kidney is connected with the pericardial sac by the renopericardial canal which is lined with heavily ciliated columnar cells.

The alimentary system consists of a digestive tract and three digestive glands. The digestive tract is covered for the most part with a simple, ciliated epithelium containing a number of goblet cells and is provided with two layers of smooth muscle fibers. The buccal gland comprises a group of mucous cells which can not be distinguished morphologically from the cells of the foot mucous gland. The salivary gland is composed of a pair of simple tubular organs with haustral-like folds in the gland proper and is morphologically different from that in *Lymnaea* sp. or in the land pulmonates where a compound tubular structure has been reported. The holocrine, simple glandular epithelium secretes PAS-positive material, which is delivered to the buccal cavity via the ducts. The liver is a compound tubular gland which delivers its secretion to the prointestine via the main hepatic duct. The simple, glandular epithelium has no basement membrane and contains two types of cells, the digestive and lime cells. The hepatic ducts are provided partly with circular, fold-like elevations which are formed by epithelial cells of varying heights.

In contrast to the findings in *Helisoma* sp., *Biomphalaria* sp. and the land pulmonates, the acini of the ovotestis of *A. glabratus* are lined with cells which can not be differentiated morphologically from fibroblasts and do not possess a basement membrane. The common collecting canal of the ovotestis is provided with a transitional epithelium and is capable of great distention. The mature germinal cells in the common collecting canal are delivered via the hermaphroditic duct to the carrefour where they are separated into the respective genital tracts. The carrefour, which has been found only in the hermaphroditic snails, is histologically an enlarged end-portion of the main duct of the albumen gland in *A. glabratus*. The vas efferens and prostatic gland are histologically similar and are the glandular portions of the male genitalia. The vas deferens, verge, vergic sac and praeputium are muscular structures and are considered devices

for copulation. The albumen gland, oviduct, nidamental gland and uterus are the glandular portions of the female genitalia. The vagina is a muscular tube and serves primarily as a copulatory organ.

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## EXPLANATION OF PLATES

Magnifications of photomicrographs and drawings are indicated in the appropriate legends for the figures. Fixatives and staining technics used for each figure are also given. Small letters indicating various detail structures are independent for each figure. Drawings were made with the aid of a camera lucida. All figures were reduced to ¾ on reproduction.

The abbreviations used in the legends are as follows: Zenker: formic acid—Zenker's fixative; Newcomer: Newcomer's fixative; PFF: formic acid—Bouin's fixative; Methyl: absolute methyl alcohol; H-E: hematoxylin-eosin; H-Phlox: hematoxylin-phloxine B; H-Az H-E: Hexatoxylin-azure II-eosin; PAS: periodic acid—Schiff reaction; Gomori: Gomori's trichrome; Azan: Mallory's trichrome; Fresh: fresh, unfixed and unstained specimen.

# PLATES

Plate 1

Fig. 1. Median, longitudinal section of a stretched snail (PFF, H-Phlox, 6x). Various positions or directions of snail body are indicated by arrows a to d; a, anterior; b, posterior or caudal; c, dorsal; d, ventral; e, location of the pseudostratified epithelium; f, location of the osphradium.

Fig. 2. Enlarged head region of Figure 1 (36x); a, lower lip; b, radular carrier; c, radular sac; d, praeputium; e, central ganglion ring; f, foot gland.

Fig. 3. Enlarged columellar muscle region of Figure 1 (36x); a, columellar muscle; b, salivary gand; c, vagina; d, uterus; e, nidamental gland; f, oviduct; g, sperm duct; h, tubular portion of the kidney; i, mantle cavity.

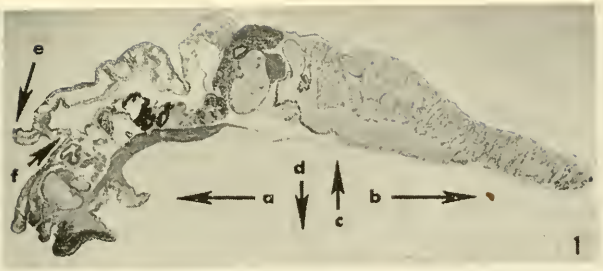


PLATE 1

Plate 2

Fig. 4. Enlarged stomach region of Figure 1 (36x); a, oviduct; b, sperm duct; c, saccular portion of the kidney; d, albumen gland; e, prointestine; f, gizzard; g, muscular wall of the gizzard.

Fig. 5. Enlarged anterior hepatic region of Figure 1 (36x); a, main hepatic duct; b, dorsal branch of the hepatic duct; c, hepatic lobules; d, midintestine.

Fig. 6. Cross section through the central ganglion ring (Zenker, H-E, 36x); a, columellar muscle; b, ganglion ring; c, radular sac; d, esophagus; e, salivary gland; f, praeputium; g, vagina; h, postintestine; i, rectal ridge; j, dorsal ridge; k, tubular portion of the kidney.

PLATE 2

Plate 3

Fig. 7. Cross section through the spermatheca (Zenker, Giemsa, 36x); a, columellar muscle; b, salivary gland; c, esophagus; d, spermatheca; e, visceral ganglion; f, vagina; g, postintestine; h, kidney ridge; i, tubular portion of the kidney.

Fig. 8. Cross section through the stomach (PFF, H-Phlox, 36x); a, gizzard; b, muscular wall of the gizzard; c, crop; d, prointestine; e, ventricle of the heart; f, pericardial sac; g, saccular portion of the kidney; h, albumen gland; i, descending crus of the midintestine; j, ascending crus of the midintestine.

Fig. 9. Cross section through the overlapping area of the liver and ovotestis (PFF, H-Az II-E, 42x); a, hepatic lobules; b, common collecting canal of the ovotestis; c, acini; d, loose vascular connective tissue.

Fig. 10. Simple epithelium of the foot surface (Zenker, H-E, 1275x).

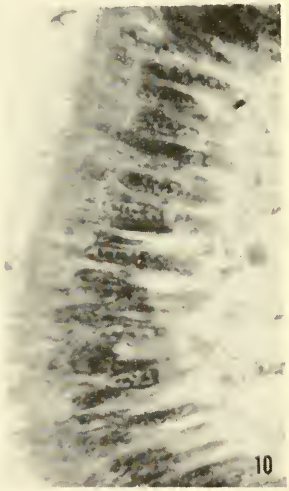



PLATE 3

Plate 4

Fig. 11. Pseudostratified epithelium of the mantle collar (Zenker, H-E, 500x); see Figure 1 e.

Fig. 12. Pigment epithelium of the mantle (Zenker, H-E, 1275x).

Fig. 13. Respiratory epithelium in the mantle cavity (Zenker, H-E, 1275x).

Fig. 14. Loose vascular connective tissue (Zenker, H-E, 500x); a, *Zirkulationslücken* of Kisker or blood space; b, smooth muscle fiber; c, crystalline concretion; d, fibroblast.

Fig. 15. Dense connective tissue (Zenker, H-E, 585x); a, blood space; b, smooth muscle fiber; c, mucous cells; d, fibroblasts.

Fig. 16. Fibroblasts (Zenker, H-E, 2200x).

Fig. 17. Pigment cells (Zenker, H-E, 1600x).

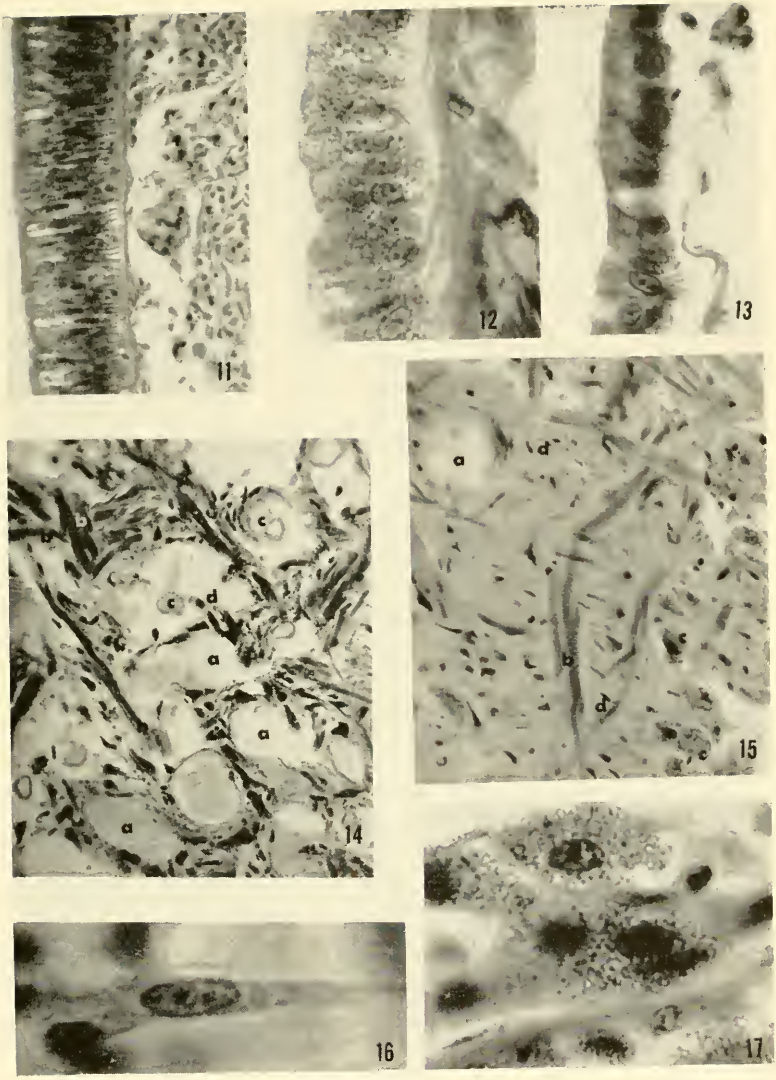



PLATE 4

Plate 5

Fig. 18. Vesicular cells (Zenker, H-E, 920x).

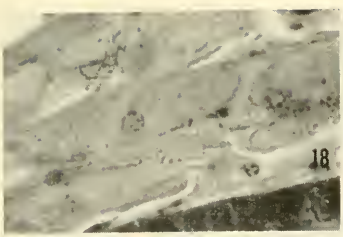
Fig. 19. Mucous cells in the foot gland (Zenker, H-E, 950x).

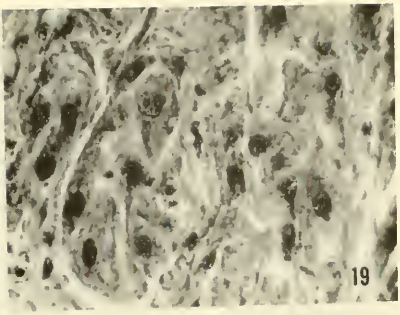
Fig. 20. Granular muscle (Zenker, H-E, 920x): a, fibroblasts.

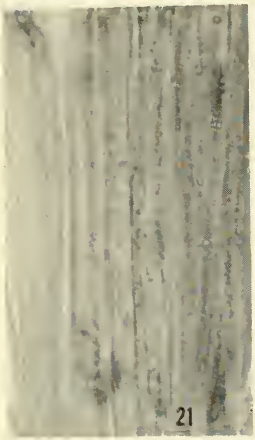
Fig. 21. Intermediate granular muscle (Zenker, H-E, 1275x).

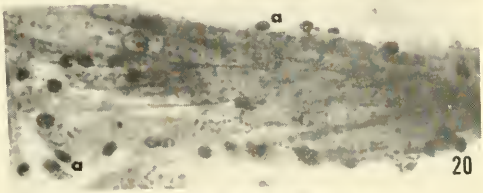
Fig. 22. Smooth muscle in the gizzard (Zenker, H-E, 920x).

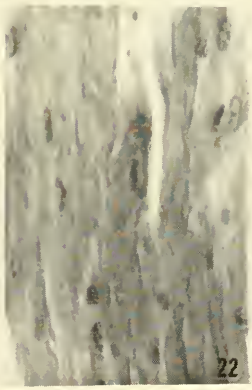
Fig. 23. Pedal ganglion and statocyst (Zenker, H-E, 292x); a, ganglion; b, statocyst; c, commissure; d, epineurium.



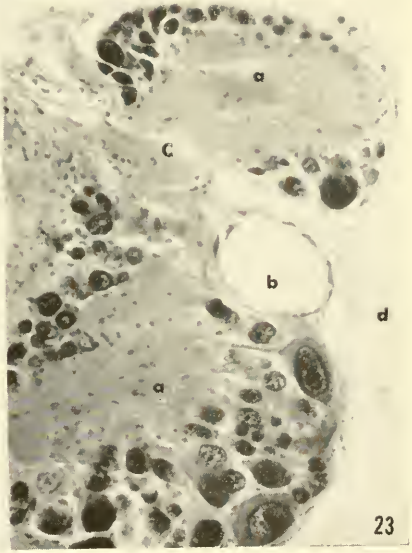




PLATE 5

Plate 6

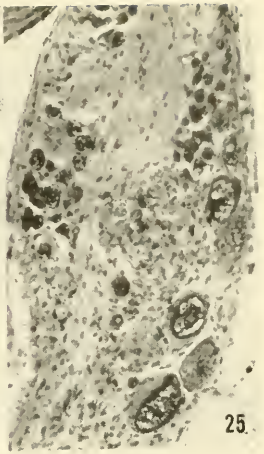
Fig. 24. Ganglion cells and statocyst containing statoliths (Zenker, H-E, 750x); a, ganglion cell with a prominent process; b, neurofibrils; c, giant cell of the statocyst; d, statoliths; e, epineurium.

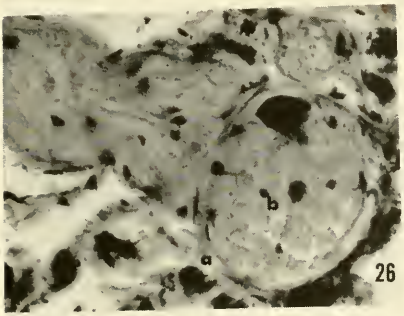
Fig. 25. Pathology of a ganglion affected by a yeast-like organism (Zenker, H-E, 300x): note hyperplasia of and nodule formation by neuroglia cells, and damaged ganglion cells.

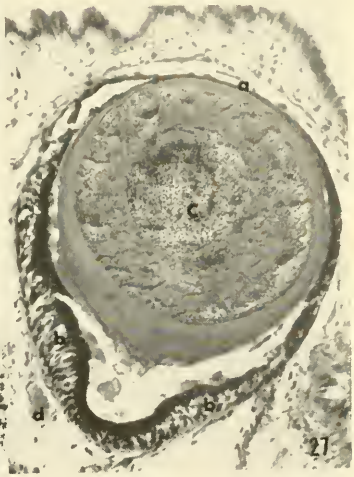
Fig. 26. Nerve (Newcomer, H-Az H-E, 585x); a, epineurium; b, neuroglia cells.

Fig. 27. Eye (Zenker, H-E, 325x); a, cornea; b, retina with its pigment layer; c, lens; d, optic nerve.

Fig. 28. Cross section of the osphradium (Zenker, H-E, 585x); a, ganglion cells.



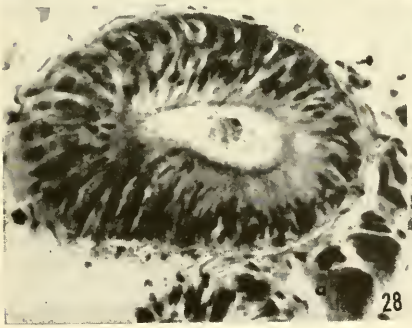




PLATE 6

## Plate 7

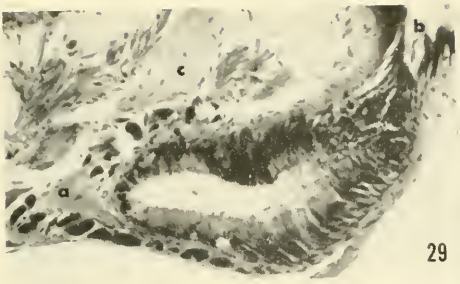
Fig. 29. Longitudinal section of the osphradium (PFF, H-Phlox, 292x); a, ganglion enveloping the osphradium; b, aperture; c, nerve.

Fig. 30. Longitudinal section of a tentacle (Zenker, H-E, 72x); a, central artery; b, dense connective tissue core containing abundant smooth muscle fibers; c, peripheral blood sinuses; d, leaf-like enlargement; e, nerve; f, peripheral sensory cells.

Fig. 31. Cross section of a tentacle (PFF, H-Az H-E, 292x); a, central artery; b, dense connective tissue core; c, peripheral blood sinuses; d, epithelium with dense pigment deposition and with cilia; e, fibroblast trabeculae.

Fig. 32. Peripheral sensory cells at the margin of the lip (Zenker, H-E, 292x); a, nerves; b, sensory cells; c, epithelium of the lip; d, blood spaces.

Fig. 33. Heart (Newcomer, Azan, 130x); a, atrium; b, ventricle c, valves; d, epicardium.

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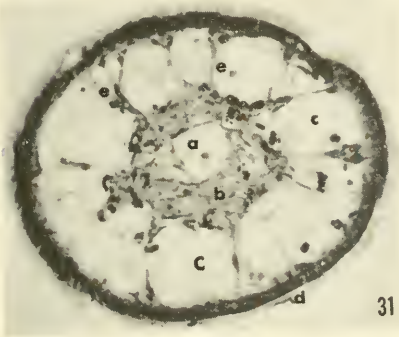


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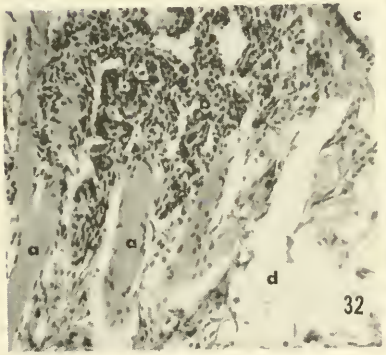


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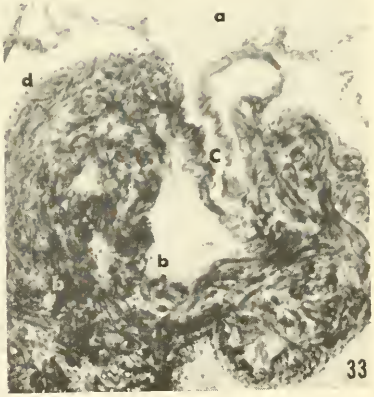


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PLATE 7

Plate 8

Fig. 34. Aortic valve (Zenker, H-Az II-E, 290x); a, lumen of the aorta; b, valve; c, lumen of the ventricle.

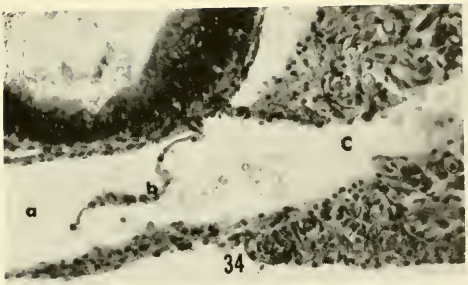
Fig. 35. Epicardium (Newcomer, H-Az II-E, 750x); a, epicardium; b, heart muscle fibers.

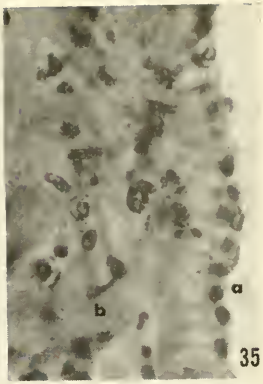
Fig. 36. Aorta (PFF, H-Az II-E, 585x); a, lining cells; b, amoebocytes; c, coagulated hemolymph.

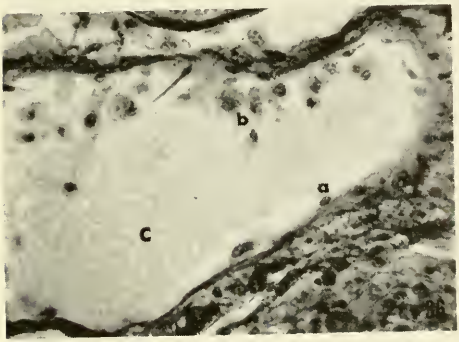
Fig. 37. Artery (Zenker, H-E, 500x); a, lining cells; b, amoebocytes; c, coagulated hemolymph.

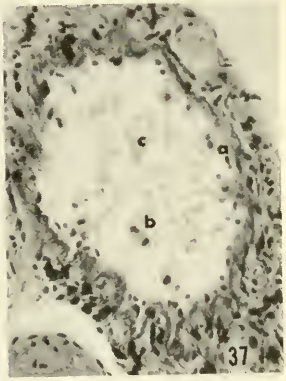
Fig. 38. Pulmonary vein (Zenker, H-E, 188x); a, vein; b, ureter; c, tubular portion of the kidney.

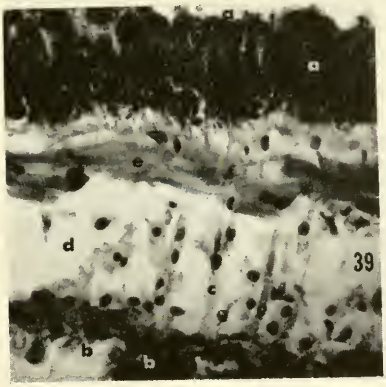
Fig. 39. Blood sinus in the mantle (Zenker, H-E, 585x); a, pigment epithelium of the mantle; b, cuboidal respiratory epithelium of the mantle cavity; c, fibroblast trabeculae; d, blood sinus; e, smooth muscle fibers.



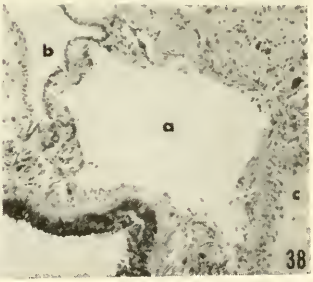




PLATE 8

Plate 9

Fig. 40. Amoebocytes in the lumen of an artery (PFF, H-Az H-E, 1600x).

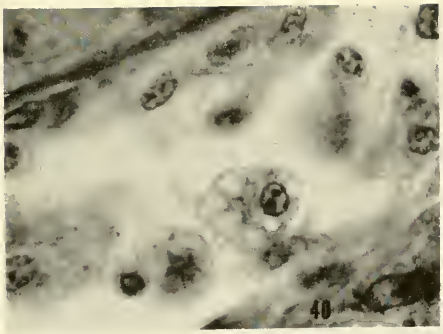
Fig. 41. Nodule formation by amoebocytes and fibroblasts and infiltration by amoebocytes (PFF, H-Az H-E, 585x); note that many of the amoebocytes contain yeast-like organisms which appear as dark dots.

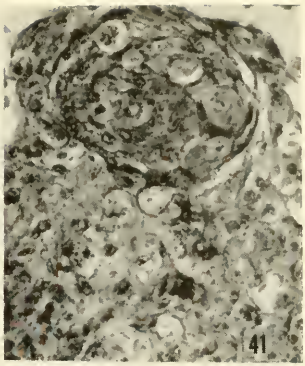
Fig. 42. Amoebocytes from the lumen of a heart (PFF, H-Az H-E, 2200x); note several yeast-like organisms in the cytoplasm.

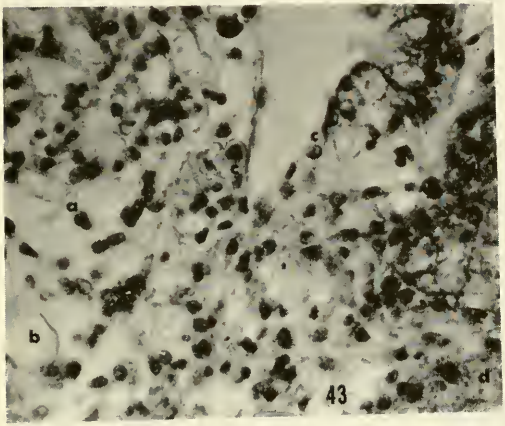
Fig. 43. Hemopoietic tissue in the wall of the saccular portion of the kidney (Zenker, H-E, 750x); a, reticular cells; b, blood spaces; c, amoebocytes; d, kidney cells.

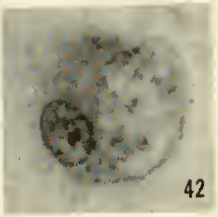
Fig. 44. Epithelium of the tubular portion of the kidney (Zenker, H-E, 585x); note the acidophilic striations in the cytoplasm.

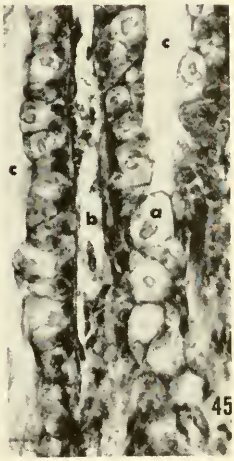
Fig. 45. Epithelium of the saccular portion of the kidney (PFF, H-Az H-E, 585x); a, crystalline concretions (urine substance of Baecker); b, blood space; c, kidney lumen.



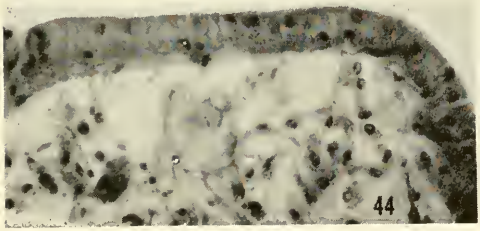




PLATE 9

## Plate 10

Fig. 46. Renopericardial canal (Zenker, Giemsa, 292x); a, kidney lumen; b, lumen of the pericardial sac; c, kidney epithelium; d, renopericardial canal.

Fig. 47. Horny jaw in the upper lip (Zenker, H-E, 250x).

Fig. 48. Cuticular epithelium in the cavity of the buccal mass (Zenker, H-E, 585x); a, cuticular layer.

Fig. 49. Vesicular cushion in the dorsal wall of the buccal mass (Zenker, H-E, 250x); a, vesicular cells; b, intermediate granular muscle; c, blood space; d, cuticular epithelium of the oral cavity.

Fig. 50. Radular sac (Zenker, H-E, 212x); a, collostyle; b, radula; c, supraradular epithelium; d, subradular epithelium; e, musculature of the buccal mass.

Fig. 51. Epithelia of the radular sac (Zenker, H-E, 585x); a, supraradular epithelium; b, subradular epithelium; c, radula; d, collostyle.

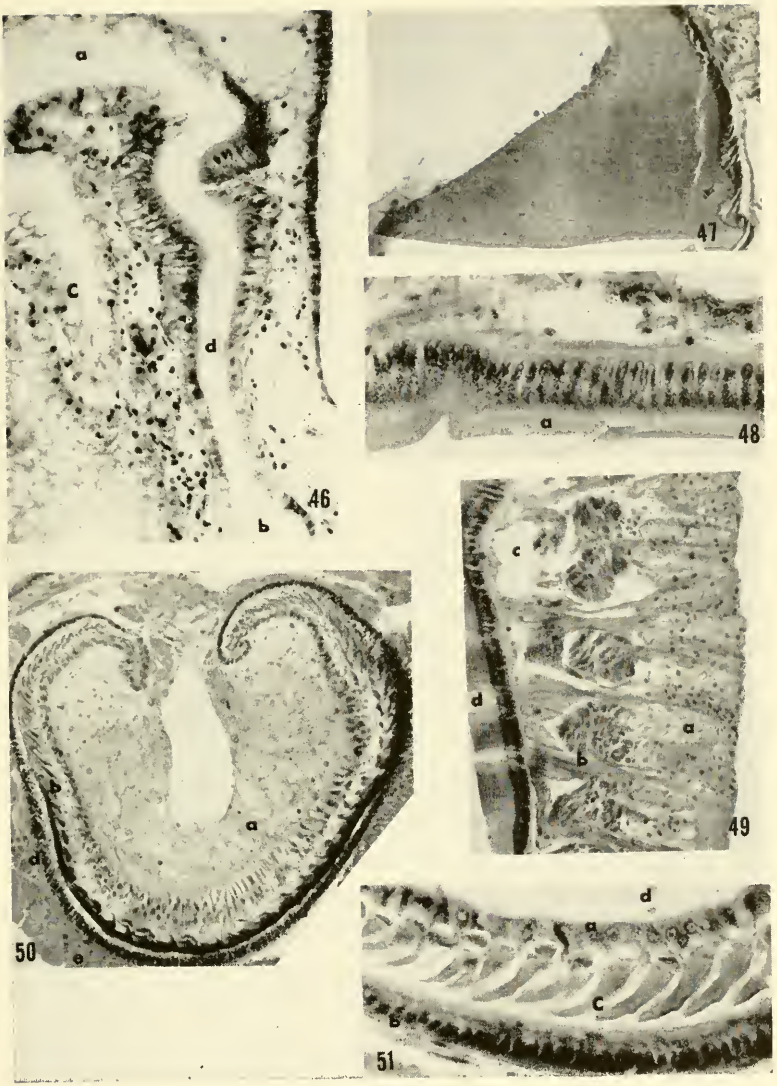



PLATE 10

Plate 11

Fig. 52. Radular carrier (Zenker, Gomori, 500x); a, vesticular cells; b, intermediate granular muscle fibers; c, epithelia.

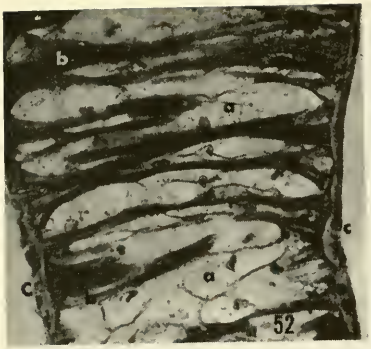
Fig. 53. Artery connecting the lumen of the radular carrier (Zenker, Gomori, 500x); a, artery; b, radular carrier; c, lumen of the radular carrier.

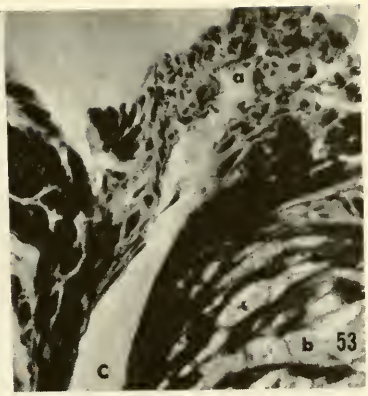
Fig. 54. Cross section of the esophagus (Zenker, H-E, 250x); a, epithelium; b, longitudinal muscle layer; c, circular muscle layer.

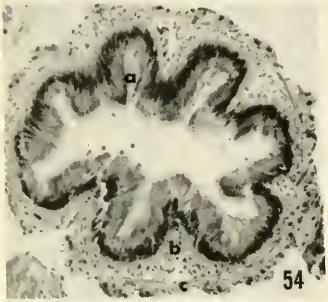
Fig. 55. Epithelium of the esophagus (Zenker, H-E, 920x).

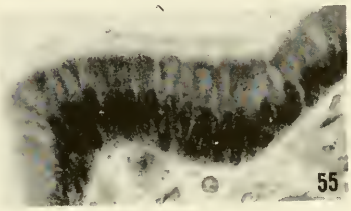
Fig. 56. Epithelium and its supportive tissue of the crop (Newcomer, Gomori, 650x).

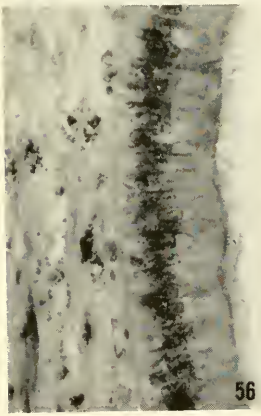
Fig. 57. Musculature in the wall of the gizzard (Newcomer, Gomori, 100x); a, cuticular epithelium.



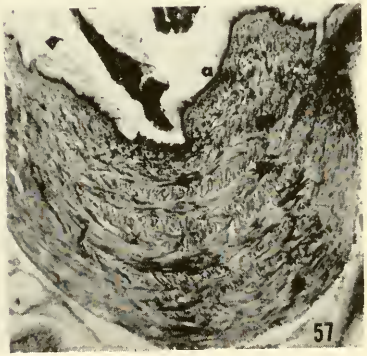




PLATE 11

Plate 12

Fig. 58. Pseudostratified epithelium of the prointestine (Newcomer, Gomori, 750x).

Fig. 59. Epithelium of the midintestine and regenerating epithelium of the liver lobule (2nd stage) (Newcomer, Gomori, 750x); a, midintestine; b, liver lobule; c, vacuole.

Fig. 60. Longitudinal section of the postintestine (Newcomer, Gomori, 100x); note the circular epithelial folds.

Fig. 61. Epithelium of the postintestine (Newcomer, Gomori, 500x).

Fig. 62. Anus (Zenker, H-E, 190x).

Fig. 63. Longitudinal section of the cecum (Newcomer, H-E, 100x); a, epithelium resembling that of prointestine; b, epithelium resembling that of hepatic duct; c, liver lobules.

PLATE 12

Plate 13

Fig. 64. Buccal gland (Newcomer, PAS, 500x); a, island of the gland cells; b, secretory material being discharged toward the epithelial sheet; c, cuticular epithelium of the oral cavity.

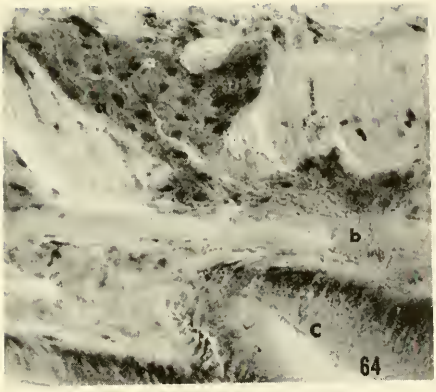
Fig. 65. Salivary gland, approximately ¼ from the opening (Zenker, H-E, 500x); note two types of epithelial cells.

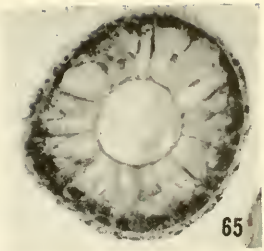
Fig. 66. Epithelium of the salivary gland proper in active secretion (Zenker, H-E, 500x); note the loss of the cell membrane on the lumen; a, saliva; b, coelomic cavity.

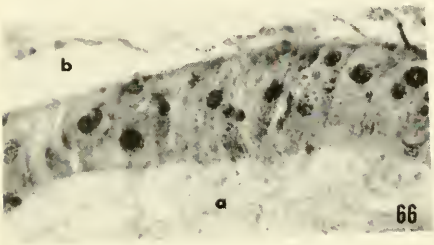
Fig. 67. Epithelium of the main hepatic duct (Newcomer, Gomori, 720x).

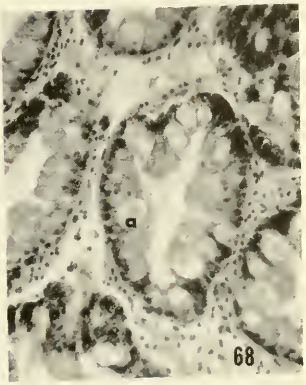
Fig. 68. Hepatic lobules with epithelium at the 3rd stage (Zenker, H-E, 292x); note the irregular lumen surface of the epithelial sheet and globular inclusion bodies of the digestive cells; a, inclusion globule.

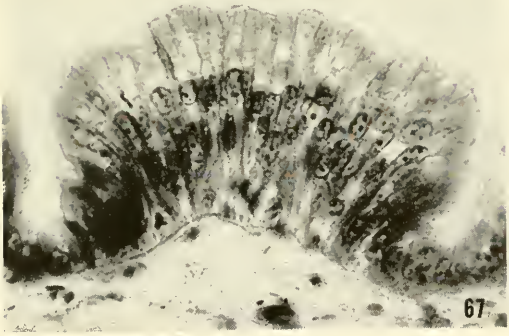
Fig. 69. Regenerating epithelium (1st stage) of the hepatic lobule (Newcomer, Gomori, 750x); note the smooth epithelial surface and the round nuclei.



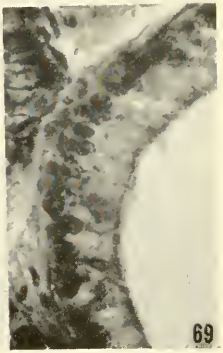




PLATE 13

Plate 14

Fig. 70. Hepatic epithelium at the 3rd stage (Zenker, H-E, 750x); a, digestive cells; b, lime cells; c, inclusion globules.

Fig. 71. Spermatogenesis (PFF, H-Az H-E, 292x); a, ovum; b, male germinal cells; c, mature spermatozoa.

Fig. 72. Mitosis in the spermatogenesis (PFF, H-Az H-E, 920x).

Fig. 73. Mature ovum (Zenker, H-E, 500x); a, nurse cells; b, male germinal cells in the adjacent acinus.

Fig. 74. Transitional epithelium of the common collecting canal of the ovotestis (Zenker, H-E, 920x).

Fig. 75. Connecting "S"-shaped tubule between the common collecting canal and the hermaphroditic duct (Newcomer, Gomori, 425x); a, lumen of the collecting canal; b, connecting tubule; c, seminal vesicle (part of the hermaphroditic duct).

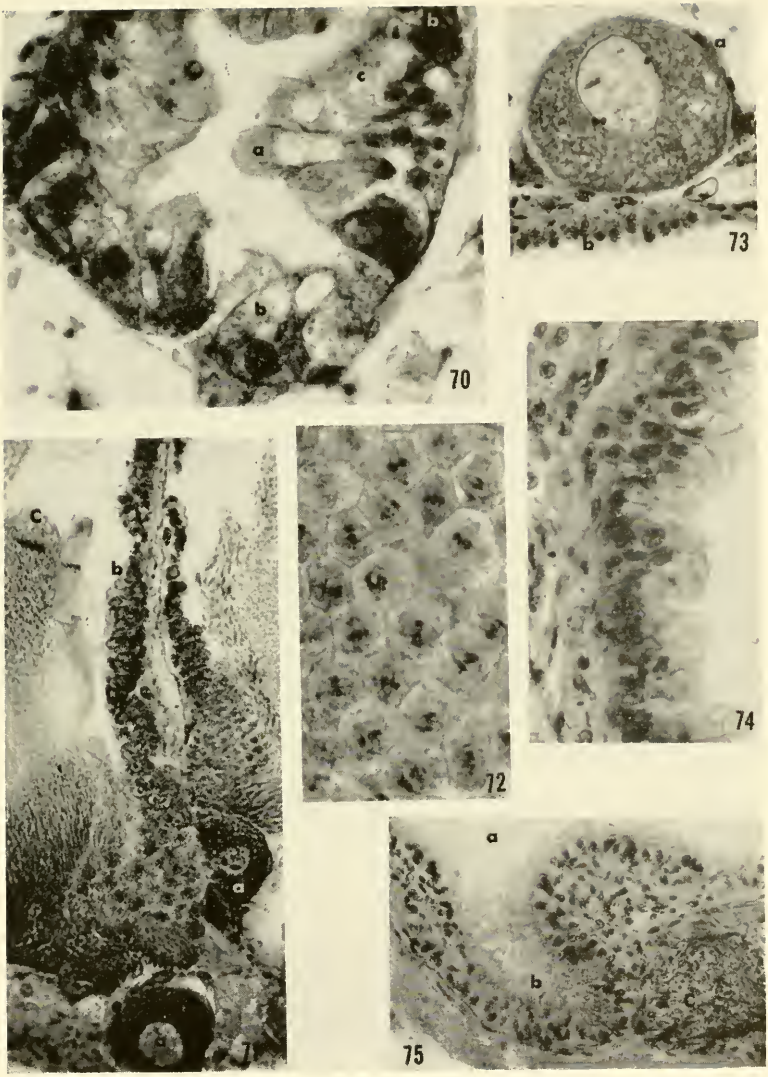



PLATE 14

## Plate 15

Fig. 76. Seminal vesicle (Zenker, H-E, 250x); note the lumen filled with numerous mature spermatozoa; a, blood space.

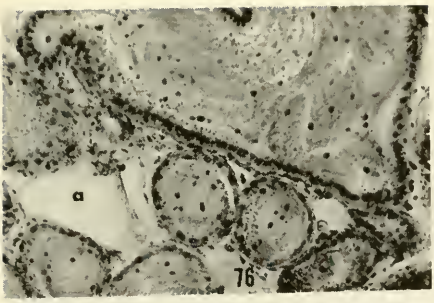
Fig. 77. Hermaphroditic duct (Zenker, H-E, 500x).

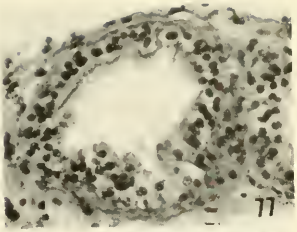
Fig. 78. Origin of the sperm duct (PFF, H-E, 430x); a, nonsecretory portion of the sperm duct; b, transition from nonsecretory to secretory portion of the sperm duct; c, carrefour; d, oviduct; e, albumen gland; f, artery.

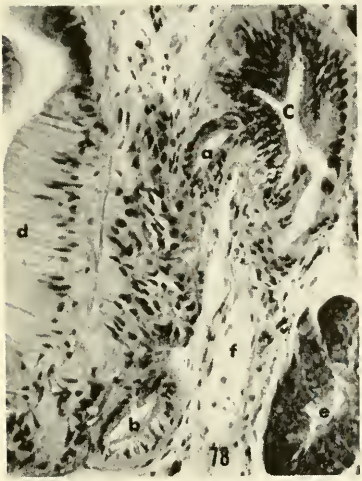
Fig. 79. Duct of the albumen gland (PFF, H-E, 325x); a, duct; b, carrefour.

Fig. 80. Epithelium of the carrefour (PFF, H-E, 320x)3; a, carrefour; b, oviduct.

Fig. 81. Secretory portion of the sperm duct (Zenker, H-E, 370x).



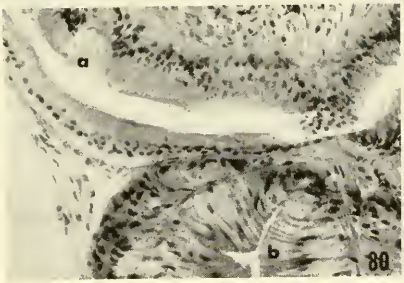


PLATE 15

Plate 16

Fig. 82. Transition from sperm duct to vas deferens (Zenker, H-E, 190x); a, sperm duct; b, vas deferens.

Fig. 83. Proximal leg of the vas deferens (Zenker, H-E, 585x).

Fig. 84. Distal leg of the vas deferens (Zenker, H-E, 500x).

Fig. 85. Verge and vergic sac (Zenker, H-E, 190x); a, verge; b, vergic sac; c, invaginated portion of the vergic sac; d, spermatheca.

Fig. 86. Cross section of the praeputium (Zenker, H-Phlox, 120x).

Fig. 87. Diaphragm of the penial complex (Zenker, H-E, 190x); a, diaphragm; b, lumen of the praeputium.

Fig. 88. Albumen gland (Zenker, H-E, 250x).

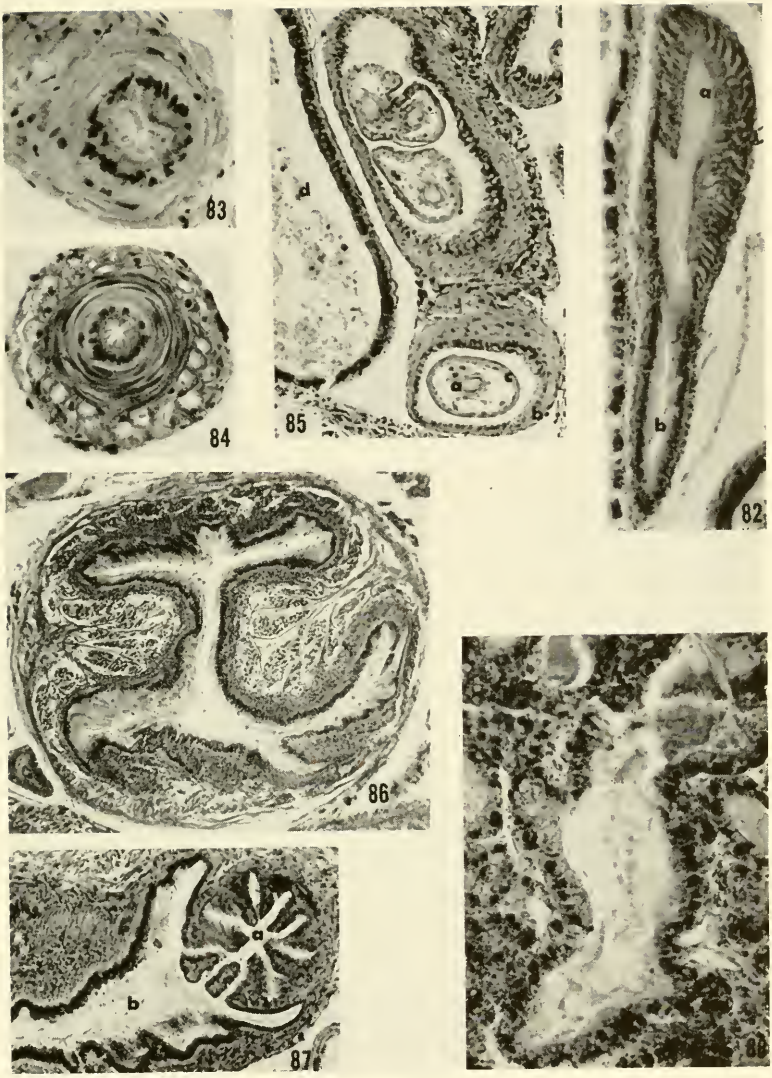



PLATE 16

Plate 17

Fig. 89. Transformation of the spermatids into mature spermatozoa (PFF, H-Az II-E, 585x); a, mature spermatozoa; b, transforming spermatids; c, Sertoli cell.

Fig. 90. Transformation of the spermatids into mature spermatozoa (Zenker, H-E, 500x); a, transforming spermatids; b, spermatogonia.

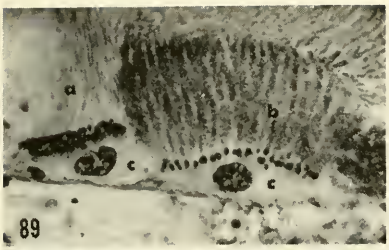
Fig. 91. Oviduct and nidamental gland (PFF, H-Phlox, 190x); a, oviduct; b, nidamental gland.

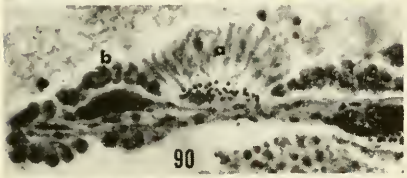
Fig. 92. Nidamental gland and uterus (PFF, H-Phlox, 180x); a, nidamental gland; b, uterus.

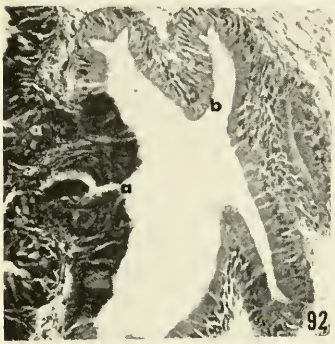
Fig. 93. Transition from the uterus to the vagina (Zenker, H-E, 295x); a, uterus; b, vagina.

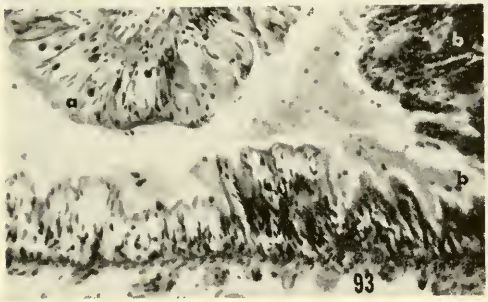
Fig. 94. Duct of the spermatheca (Zenker, H-E, 585x); a, mucous cells.

Fig. 95. Vagina (Zenker, H-E, 190x).



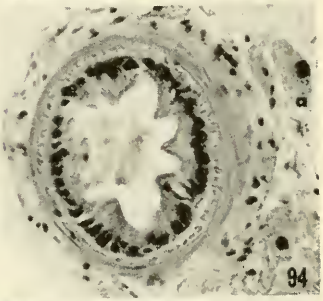


PLATE 17

## Plate 18

Fig. 96. Mature spermatozoa (Methyl, Giemsa, 3600x).

Fig. 97. Separation of the male and female genital tracts from the hermaphroditic duct (Fresh, 45x); a, hermaphroditic duct; b, duct of the albumen gland; c, carrefour; d, sperm duct; e, oviduct.

Fig. 98. Slightly stretched female genital tract (Fresh, 9.9x); a, oviduct; b, nidamental gland; c, uterus; d, vagina; e, spermatheca; f, duct of the spermatheca.

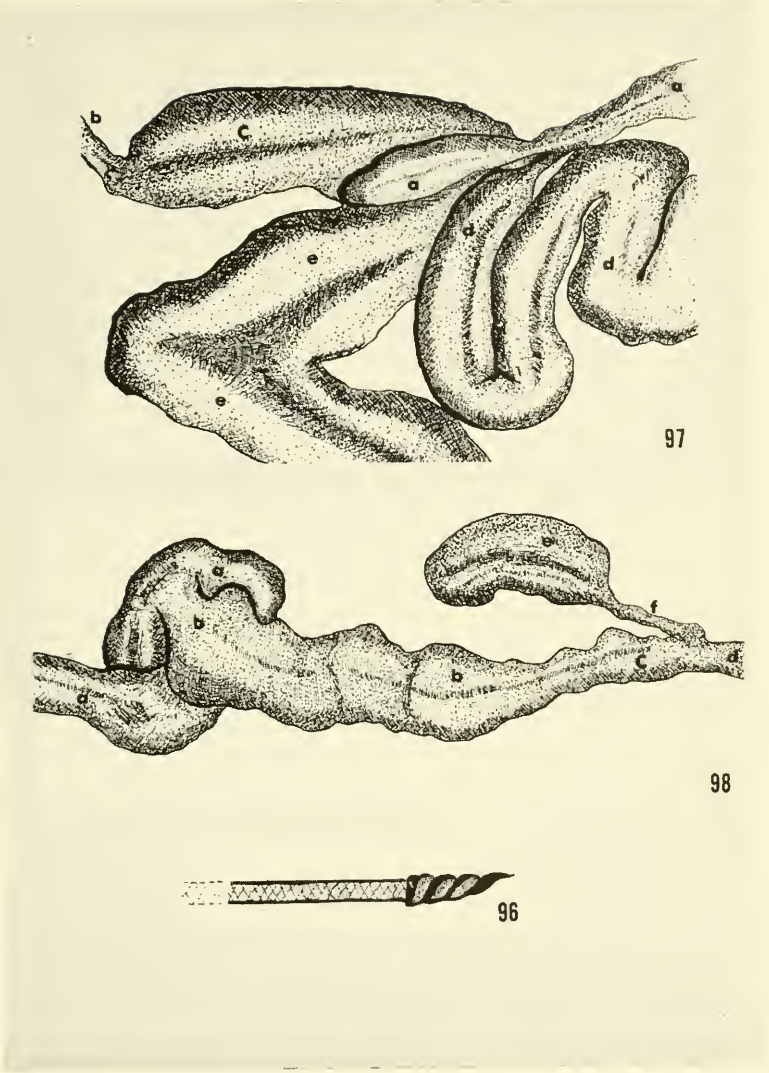



PLATE 18

**Bulletin of the Museum of Comparative Zoology**

AT HARVARD COLLEGE

Vol. 119, No. 4

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# STUDIES ON THE ANT FAUNA OF MELANESIA III. RHYTIDOPONERA IN WESTERN MELANESIA AND THE MOLUCCAS. IV. THE TRIBE PONERINI

By E. O. Wilson

Biological Laboratories, Harvard University

CAMBRIDGE, MASS., U. S. A.

PRINTED FOR THE MUSEUM

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MUSEUM OF COMPARATIVE ZOOLOGY
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Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

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No. 4 — *Studies on the Ant Fauna of Melanesia*[1]

*III. Rhytidoponera in Western Melanesia and the Moluccas*

*IV. The Tribe Ponerini*

By E. O. Wilson
Biological Laboratories, Harvard University

## III. RHYTIDOPONERA IN WESTERN MELANESIA AND THE MOLUCCAS

*Rhytidoponera* is a large genus almost entirely confined to Australia and Melanesia. Eleven species are known from western Melanesia, and several of these are among the most abundant and adaptable ants of the region. However, only two, *araneoides* and *nexa,* extend much beyond the limits of New Guinea, *nexa* occurring in addition on Waigeo and New Britain and *araneoides* ranging beyond to the Philippines and Solomons. No member of the genus is known from either the New Hebrides or Fiji Islands. New Caledonia harbors a distinctive endemic fauna of its own,[2] consisting of at least seven species, which are not closely allied to any of the western Melanesian species (with the possible exception of *R. inops*) but instead appear to represent stocks independently derived from the Australian fauna.

Two of the eleven known New Guinea species, *araneoides* and *purpurea,* have been recorded in addition from North Queensland. The remaining eight seem individually distinct from known Australian species, but have not otherwise diverged beyond the species or species-group level. Below are listed the New Guinea species, arranged into provisional species-groups and with new synonymy added.

### Group of *R. araneoides* (Le Guillou)

*araneoides* (Le Guillou)
=*Ectatomma rugosa* Fr. Smith
=*Ectatomma* (*Rhytidoponera*) *froggatti* Forel

[1] Previous parts of this series appeared in the Bulletin of the Museum of Comparative Zoology, vol. 118, pp. 99-153, 1958.

[2] The New Caledonian *Rhytidoponera* are currently being revised by Dr. W. L. Brown as part of his larger study of the world Ectatommini.

=*Rhytidoponera araneoides* var. *impressinodis* Stitz
=*Rhytidoponera araneoides* var. *ecramensis* Viehmeyer

Group of *R. celtinodis* Wilson

*celtinodis* Wilson

Group of *R. inops* Emery

*inops* Emery
=*Rhytidoponera striata* Donisthorpe

Group of *R. purpurea* Emery

*aenescens* Emery
*purpurea* Emery

Group of *R. strigosa* (Emery)
*abdominalis* Viehmeyer
*laciniosa* Viehmeyer
=*Rhytidoponera laciniosa* subsp. *petiolata* Viehmeyer
*nexa* Stitz
=*Rhytidoponera strigosa* var. *major* Stitz
=*Rhytidoponera gagates* Donisthorpe
=*Rhytidoponera gagates* subsp. *waigeuensis* Donisthorpe
*rotundiceps* Viehmeyer
*strigosa* (Emery)
=*Rhytidoponera subcyanea* subsp. *intricata* Emery
=*Rhytidoponera strigosa* var. *curvata* Stitz
=*Rhytidoponera schlaginhaufeni* Viehmeyer
=*Rhytidoponera nitens* Donisthorpe
*subcyanea* Emery
=*Rhytidoponera subcyanea* subsp. *transversiruga* Emery
=*Rhytidoponera subcyanea* var. *aruana* Karawajew
=*Rhytidoponera wallacei* Donisthorpe

*Key to the species, based on the worker caste*

1. Petiolar node tapering dorsally to form a thin, emarginate, transverse crest; the posterior nodal face bearing a deep median longitudinal

furrow along most of its length ..... *celtinodis* Wilson

Seen from the side the petiolar node is either evenly rounded above or else bears a broad flat dorsal face; the posterior nodal face lacking a median longitudinal furrow ..... 2

2. Small species, head width measured across and including the eyes 1.47 mm or less; occipital border strongly concave when viewed in perfect full face ..... *inops* Emery

Medium to large species, head width exceeding 1.60 mm; occipital border straight or convex when viewed in full face ..... 3

3. Almost the entire body surface emitting distinct metallescent reflections when viewed in sunlight or ordinary artificial light ..... 4

At the most the gaster emits feeble bluish reflections (occasional series of *strigosa*); usually the body completely lacks metallescent reflections of any sort ..... 6

4. Body reflections aenescent (brassy) or subaenescent ..... *aenescens* Emery

Body reflections bluish or purplish ..... 5

5. Striae of first gastric tergite transverse and nearly straight ..... *subcyanea* Emery

Striae of first gastric tergite mostly semicircular and concentrically arranged ..... *purpurea* Emery

6. First gastric tergite very finely and densely striate, ten or more striae being included in a single 0.10 mm transect; in some series the striae are obsolescent in the central area of the tergite, being largely replaced there by fine shagreening ..... *araneoides* (Le Guillou)

Sculpturing of first gastric tergite different, consisting of striae, costulae, or rugae which are much coarser and more widely spaced than described above ..... 7

7. Larger species, head width across and including eyes 2.14 mm or greater; if head width is less than 2.28 mm, then sculpturing of anterior third of pronotal dorsum (exclusive of collar) consists entirely of transversely oriented, non-reticulate costulae ..... 8

Smaller species, head width across and including eyes 2.10 mm or less; anterior third of pronotal dorsum always rugoreticulate, the rugae rarely showing a predominant transverse orientation ..... 9

8. (Based on a single syntype). Head width 2.14 mm; anterior third of pronotal dorsum (exclusive of collar) covered by transverse, non-reticulate costulae, posterior two-thirds covered by narrowly arcuate, concentric, non-reticulate costulae with anterior apices (Torricelli Mts., N-E. New Guinea) ..... *abdominalis* Viehmeyer

(Based on numerous series from over entire range). Head width 2.28 mm or greater; most or all of pronotal dorsum covered by rugoreticulum, of which only a small part shows a transverse or arcuate orientation (widespread, Waigeo to New Britain) *nexa* Stitz

9. Occipital region evenly rounded, completely lacking a torus or any other form of gibbosity; petiolar node seen from the side low and rounded, its anterior face much shorter than the anterior peduncle is wide .... *rotundiceps* Viehmeyer

Occipital region bearing either a transverse torus or paired lateral gibbosities; petiolar node seen from the side relatively high and subrectangular in shape as in most other Papuan members of the genus, its posterior face as long as the anterior peduncle is wide, or longer .... 10

10. Sculpturing of first gastric tergite consisting of even, relatively unwavy striae distributed for the most part in concentric semicircles around a center located somewhere on the tergital midline .... *strigosa* Emery

Sculpturing of first gastric tergite consisting of very wavy striae, which are only occasionally distributed in semicircles as described above, and are more often either transversely oriented or uniformly reticulate in pattern .... *laciniosa* Viehmeyer

### Rhytidoponera abdominalis Viehmeyer, n. status

*Rhytidoponera subcyanea* subsp. *abdominalis* Viehmeyer, 1912, Abh. Zool.-anthrop.-ethn. Mus. Dresden, 14: 4, fig. 1, worker. Type locality: Torricelli Mts., N-E. New Guinea. (Syntype examined — Viehmeyer Coll., Dresden).

Through the courtesy of the officials of the Staatlichen Museum für Tierkunde, Dresden, I have been able to examine a syntype of this problematical form. In my present opinion *abdominalis* represents a distinct species morphologically intermediate between *strigosa* Emery and *nexa* Stitz. It differs from both of these species in the sculptural characters given in couplet 8 of the key, and as indicated in couplet 7 it is intermediate in size between them. Its gastric costulation is relatively widely spaced, closely resembling *nexa* as opposed to *strigosa*. Its petiolar node is much thicker than that of New Guinea mainland *nexa*, surpassing even that of most *strigosa*, but is not nearly so extreme as in the Waigeo variant of *nexa* (*q.v.*).[1]

### Rhytidoponera aenescens Emery

*Rhytidoponera aenescens* Emery, 1900, Természetr. Füz., 23: 312, worker. Type locality: Lemien, near Berlinhafen (= Aitape), N-E. New Guinea.

[1] As a note to aid future comparisons, the outline of the node of the *abdominalis* type is almost identical to that of the larger of two *strigosa* workers from my accession no. 993, deposited in the MCZ.

Known from type material only. According to Emery in the original description, this species differs from the related *R. purpurea* Emery not only in color but also in minor details of body form and sculpturing. The head is said to be more rounded, the mesonotum less convex, the rugae of the head more reticulate and less longitudinally oriented, etc.

### Rhytidoponera araneoides (Le Guillou)

*Ponera araneoides* Le Guillou, 1842, Ann. Soc. Ent. Fr., 10: 317, worker. Type locality: Solomon Islands. (Holotype examined —Paris Museum).

*Ectatomma rugosa* Fr. Smith, 1859, Jour. Linn. Soc. Zool., 3: 143-144, worker, male. Type locality: Aru. *Nec Ectatomma rugosa* Fr. Smith, 1865, *ibid.*, p. 71, worker. (Holotype examined — British Museum).

*Ectatomma* (*Rhytidoponera*) *froggatti* Forel, 1910, Rev. Suisse Zool., 18: 10, worker. Type locality: Solomon Islands. (Syntype examined — Forel Coll.). NEW SYNONYMY.

*Rhytidoponera araneoides* var. *impressinodis* Stitz, 1912, Sitzber. Ges. Naturf. Freunde Berlin, p. 498, fig. 2, worker. Type locality: Ceram. NEW SYNONYMY.

*Rhytidoponera araneoides* var. *ceramensis* Viehmeyer, 1914, Ent. Mitt., 3: 112, worker. Type locality: West Ceram. NEW SYNONYMY.

*Rhytidoponera* (*Rhytidoponera*) *araneoides* var. *froggatti*, Mann, 1919, Bull. Mus. Comp. Zool., 63: 286-288, male.

*Material examined.* MOLUCCAS: Ceram (D'Albertis). N-E. NEW GUINEA: Nadzab, Markham Valley (Wilson, nos. 1088, 1096, 1100); lower Busu River (Wilson, no. 952); Finschhafen (E. S. Ross). PAPUA: Karema, Brown River (Wilson, nos. 557, 564, 566, 591). ADMIRALTIES: Los Negros (G. E. Bohart). BOUGAINVILLE: Mosigeta (E. J. Ford, Jr.); Kihili, near Buin (Ford); Boku (Ford); Kokura, 690 m. (Ford). FLORIDA: Tulagi and Maliali (W. M. Mann). MALAITA: Auki, near Fourafi (Mann). I have also identified material of this species from Los Negros, Philippines (J. W. Chapman), comprising the westernmost record for the genus.

*Taxonomic notes.* Two worker characters, sculpturing of the first gastric tergite and shape of the petiolar node, show marked geographic variation. These are described separately below.

In eastern New Guinea, the first gastric tergite is covered by fine, dense, transverse striae, which tend to become obsolescent in the central portion of the tergite and are often replaced by

shagreening there. In the west, the single Ceram specimen examined differs only in that the striae tend to become obliquely oriented. The single Philippine series examined is essentially similar in sculpturing to those from New Guinea. The single Admiralties series differs in having the striae as well developed centrally as peripherally. The Solomons material (including the holotype of the species) has strongly developed, somewhat coarser transverse striae over the entire tergital surface.

The petiolar node of the Solomons series is somewhat thicker than that of New Guinea material, while material from the Admiralties is intermediate in this condition. The Ceram specimen has a node about as thick as in New Guinea material, but differs in that its anterior dorsal nodal border seen from a posterior oblique view is concave, instead of convex. The Philippine specimens have unusually thin nodes, which combined with very weak nodal sculpturing, strongly distinguishes them from the remainder of the *araneoides* material; future revisers may consider these differences of sufficient magnitude to warrant specific status for the Philippine population.

*Ecological notes.* At Nadzab *araneoides* was found to be very common in open, dry evergreen woodland. At Karema it appeared to be restricted to clearings in the rain forest, while at the Busu River it was encountered only in open "kunai" grassland well away from the rain forest. In the eastern Solomons, on the other hand, Mann (1919) seems to imply that *araneoides* is a rain forest dweller; he associates it with such normally deep-forest inhabitants as *Myopopone castanea* and *Rhopalothrix malua.* Future field workers should investigate this matter further to see whether *araneoides* really undergoes a change in habitat preference in the differing biotic-environmental conditions of the Solomons.

Two nests were found by the author in New Guinea. One was beneath a rotting log on the ground; galleries extended into both the wood of the log itself and into the soil underneath. Another nest was found in open soil in a forest clearing and was marked externally by a single vertical gallery approximately ten millimeters in diameter.

Workers were found foraging away from their nests during both the day and early night. In most cases they were on the

ground, but on one occasion a single worker was found on a tree trunk several feet from the ground, and on two occasions (at Nadzab) workers were found attending extrafloral nectaries of an undetermined herbaceous plant.

Workers are relatively docile and timid, tending to run and hide when the nest is disturbed, but are capable of delivering a painful sting when handled.

### Rhytidoponera celtinodis Wilson, n. sp.

*Diagnosis.* Evidently most closely related to the Papuan species *R. strigosa* Emery, but easily distinguished from this and all other known Papuan species by its dorsally acute, posteriorly furrowed petiolar node. Certain Australian species, including *R. aurata* (Roger), *R. nodifera* Emery, *R. punctigera* Crawley, *R. rufonigra* Clark, and *R. taurus* Forel, possess more or less similar features in the node, but differ from *celtinodis* in other details of node structure, in their greater total size, and in many details of body sculpturing.

*Holotype worker.* HW 1.51 mm, HL 1.79 mm, SL 2.04 mm, CI 84, SI 135, PW 1.11 mm, dorsal petiole width 0.52 mm. Mandibular dentition (apparently typical for the species) consists of a well developed apical tooth, followed serially by a smaller subapical tooth (the tip of which is 0.08 mm from that of the apical tooth), next by several denticles, then by a well developed tooth (the tip of which is 0.26 mm from that of the apical tooth), and finally by an even series of denticles, which occupy the basal 0.35 mm of the masticatory border. Eye in exact side view prominent but forming considerably less than a half-circle. Occipital torus weakly developed, consisting of nothing more than raised horizontal rugae that stand out above the surrounding cephalic rugoreticulum. Alitrunk very similar in form to that of *R. strigosa* Emery. Petiolar node seen directly from the side with feebly concave anterior border, strongly convex posterior border, and acute summit. Viewed anteroposteriorly the dorsal border is strongly emarginate, the lateral corners evenly rounded. Viewed from directly above, the transverse dorsal crest is seen to be as wide as the basal portion of the node. A broad longitudinal sulcus runs from the crest posteriorly for more than two-thirds the length of the posterior node face.

Sculpturing approximately as in *R. strigosa:* mandibles, scapes, and tibiae longitudinally striate; coxae and femora predominantly transversely striate; entire head, alitrunk, and petiolar node coarsely rugoreticulate. First gastric tergite covered by semicircular, concentrically arranged striae with a "center" at the midpoint of the posterior tergital margin. Second gastric tergite similarly sculptured, but the "center" of concentricity is located on the tergital midline a short distance anterior to the posterior tergital border, and the striae posterior to it are straight and longitudinally oriented. Succeeding gastric tergites covered mainly by fine, transverse striae, their surfaces feebly shining.

Pilosity similar to that of *strigosa:* consisting almost entirely of relatively abundant erect hairs distributed evenly over the body and appendages, somewhat longer than that of *strigosa,* the longest hairs on the anterior scape surface about 1.1 mm long, those on the dorsal alitruncal surface about 1.3 mm long. Pubescence as in *strigosa,* i.e. sparse and predominantly appressed.

Body and antennae concolorous medium reddish-brown, coxae brownish-yellow, remainder of the legs light to medium brownish-yellow.

*Paratype workers.* HW 1.49-1.58 mm, HL 1.79-1.86 mm, SL 1.96-2.17 mm, CI 83-85, SI 132-137, PW 1.11-1.16 mm.

*Material examined.* NETH. NEW GUINEA: Maffin Bay, holotype and three nidoparatype workers (Sept. 10, 1944; E. S. Ross), plus three additional paratype workers (July 1 and Sept. 14, 1944; Ross). The holotype and three paratypes have been returned to Dr. Ross for deposition in the collection of the California Academy of Sciences. The three remaining paratypes have been deposited in the Museum of Comparative Zoology.

### Rhytidoponera inops Emery

*Rhytidoponera inops* Emery, 1900, Természetr. Füz., 23: 312, worker. Type locality: N-E. New Guinea.

*Rhytidoponera inops,* Emery, 1912, Deutsch. Ent. Z., p. 80, worker.

*Rhytidoponera* (*Chalcoponera*) *striata* Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)1: 744-745, worker. Type locality: Maffin Bay, Neth. New Guinea. NEW SYNONYMY.

*Material examined.* NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N-E. NEW GUINEA: Chimbu Valley, Bismarck Range, 1500-2300 m. (P. J. Darlington); Didiman Creek, Lae (Wilson, no. 980); Bolingbangeng (=Boingbongen), 900-1000 m. (Wilson, no. 728); Maroruo, 900 m. (Wilson, no. 729).

*Taxonomic notes.* The material studied varies considerably in size, coloration, and sculpturing. The Maffin Bay workers are smaller and more lightly colored than the other series. In the Chimbu Valley workers the pronotal sculpturing contains a greater preponderance of longitudinally oriented rugae and less of the irregular, reticulate pattern shown by the other series; in this respect it agrees more closely with the characterization of *inops* given in Emery's original description.

*Ecological note.* All of the author's collections consisted of stray workers found foraging during the day on the floor of second-growth rain forest.

### Rhytidoponera laciniosa Viehmeyer

*Rhytidoponera laciniosa* Viehmeyer, 1912, Abh. Zool.-anthrop.-ethn. Mus. Dresden, 14: 5, figs. 3, 3a, worker. Type locality: Torricelli Mts., N-E. New Guinea. (Syntype examined — Forel Coll.)

*Rhytidoponera laciniosa* subsp. *petiolata* Viehmeyer, 1912, *ibid.*, p. 5, fig. 4, worker. Type locality: Torricelli Mts., N-E. New Guinea. NEW SYNONYMY.

*Material examined.* N-E. NEW GUINEA: Torricelli Mts. (syntype); lower Busu River (Wilson, nos. 704, 872, 967, 988, 1002, 1007, 1008, 1026, 1031, 1044); Bolingbangeng to Nganduo, 900-1000 m. (Wilson, no. 731); Nganduo, 1000 m. (Wilson, no. 733); Zingzingu, 1100 m. (Wilson, nos. 761, 765, 766); Gemeheng, 1200-1300 m. (Wilson, nos. 778, 780, 782, 787, 788); Ebabaang, 1300-1400 m. (Wilson, no. 828); Finschhafen (N. G. L. Wagner).

*Taxonomic notes.* The sculpturing of the first gastric tergite is exceedingly variable in this species. It ranges from a coarse, irregular rugoreticulum to a pattern of concentric rugae with the center of concentricity located somewhere along the tergital midline. Most of the variation is encompassed by the series from a single locality, the lower Busu River.

*Ecological notes.* On the Huon Peninsula this species is abundant through a wide range of elevation. It occurs from lowland rain forest (Busu River) to clearings in true midmountain rain forest at more than 1000 meters elevation. However, it is not known to extend into the dry bottomland forests of the nearby Markham Valley.

Nesting habits are also quite variable. Colonies were found most commonly in and under very rotten "Passalus-stage" logs on the forest floor, and occasionally under loose bark on the upper surface of very large rotting logs. At the Busu River a small colony was found in large cavities of an old, hard polyphore fungus growing on top of a large log. Another Busu River colony occupied large cavities in the root-mass of an epiphytic fern growing on the trunk of a small tree a little more than a meter from the ground. Between Bolingbangeng and Nganduo, at 900-1000 m., a colony was nesting in the clayey soil of a vertical bank beside a native trail; a single large entrance gallery extended horizontally into the bank.

Colonies usually contain between 50 and 200 workers. Despite diligent searching, no queen or other recognizable female reproductive was ever uncovered. Males were collected in a nest at Gemeheng during mid-April, 1955.

At the Busu River, workers were often encountered foraging on the forest floor during the day. Near Zingzingu several individuals were found, along with workers of *Diacamma rugosa* (Le Guillou), on low herbaceous vegetation at the side of a native trail in open second-growth forest. They appeared to be attending extrafloral nectaries.

### Rhytidoponera nexa Stitz, n. status

*Rhytidoponera strigosa* var. *nexa* Stitz, 1912, Sitzber. Ges. Naturf. Freunde Berlin, p. 500, fig. 4, worker. Type locality: New Guinea (Lauterbach leg.). (Syntypes examined — Zoologisches Museum, Berlin.)

*Rhytidoponera strigosa* var. *major* Stitz, 1912, *ibid.*, p. 501, worker. Type locality: New Guinea (Kaiserin-Augusta-Fluss Exped., Bürgers leg.). (Holotype examined — Zoologisches Museum, Berlin.) NEW SYNONYMY.

*Rhytidoponera gagates* Donisthorpe, 1941, Trans. Roy. Ent. Soc. London, 91(2): 51-52, worker. Type locality: Mt. Baduri, Japen I., Neth. New Guinea. NEW SYNONYMY.

*Rhytidoponera gagates* subsp. *waigeuensis* Donisthorpe, 1942, Ann. Mag. Nat. Hist., (11)9: 703, worker. Type locality: Camp Nok, 800 m., Waigeo. *Ibid.*, (11)10: 435, male, doubtfully associated. (Syntype examined — MCZ). NEW SYNONYMY.

*Material examined.* WAIGEO: (*waigeuensis* syntype). NETH. NEW GUINEA: Maffin Bay (E. S. Ross; 6 series). N-E. NEW GUINEA: Wewak (Toyohi Okada). PAPUA: Bisianumu, 500 m. (Wilson, nos. 617, 618, 659, 667). NEW BRITAIN: St. Paul's, Bainings Mts., Gazelle Pen., 350 m. (J. L. Gressitt).

*Taxonomic notes. R. nexa* can be easily distinguished from the sympatric *R. strigosa* and *R. laciniosa* by the characters given in couplet 7 of the key. The holotype of *strigosa* var. *major* is evidently conspecific with *nexa*. It differs from the *nexa* syntypes only in the possession of a slightly thicker petiolar node, which nevertheless falls within the extreme range of variation of series from Maffin Bay.

The Maffin Bay series are nearly or completely identical in external morphology with the *nexa* syntypes. The two forms described by Donisthorpe, *gagates* and *gagates* subsp. *waigeuensis*, are in my opinion nothing more than peripheral geographic variants of *nexa*. Equal or greater deviation from "typical" *nexa* is shown by the recently acquired series from Papua and New Britain. The total geographic variation, as it is now understood, is summarized in the sections to follow.

## Waigeo

A syntype of *waigeuensis* Donisthorpe in the MCZ differs from "typical" *nexa* (*nexa* syntypes and Maffin Bay series) as follows:

(1) The cephalic rugae tend less to form into a reticulum.

(2) The sculpturing (striation) of the first two gastric tergites is stronger. On the second tergite, the center of concentricity of the striae is located approximately 0.40 mm anterior to the posterior tergital border and is enclosed by striae; in the *nexa* syntypes and Maffin Bay series the center of concentricity is approximately 0.25 mm anterior to the posterior border and is not enclosed posteriorly.

(3) The petiolar node is distinctly thicker and with more oblique anterior and posterior faces than in the *nexa* syntypes and Maffin Bay series. The surface formed jointly by the anterior node face and dorsal surface of the anterior peduncle is much less concave.

Japen Island

When Donisthorpe described *gagates* and *gagates* subsp. *waigeuensis* he was evidently unaware of the relationship of these forms to *nexa,* but in the description of *waigeuensis* he made the following note which suggests that at least in gastric sculpturing *gagates* is closer to the *nexa* types than to *waigeuensis*: "[in *waigeuensis*] the striae on the first two segments of the gaster are considerably more impressed and those on the post-petiole much more curved [than in *gagates*]."

New Britain

A single worker from the Bainings Mountains differs from the material described above in the following two characters:

(1) The center of concentricity of the striae of the second gastric tergite is located in the center of the tergite.

(2) The petiolar node is intermediate in thickness and shape between those of the *nexa* and *waigeuensis* types.

It is noteworthy that the petiolar node shape shows what may be a "central-peripheral" pattern of geographic variation. The form of the node tends to converge on Waigeo and New Britain, at the extreme opposite ends of the range of the species.

Bisianumu, Papua

Workers from this locality differ from the rest of the *nexa* series in the following characters:

(1) The circumocular rugae show a more regular concentric orientation.

(2) The anterior pronotal rugae show a more regular transverse orientation.

(3) Three of the four Bisianumu series are dark reddish-brown in color, while the fourth is a shade darker, or blackish-brown. *Nexa* series from other localities are almost all blackish-brown.

*Ecological notes.* At Bisianumu, workers were found during the day actively running over the floor of second-growth foothills rain forest.

A single male tentatively determined as this species was collected by J. L. Gressitt at St. Paul's, Bainings Mts., New Britain on September 5, 1955.

### Rhytidoponera purpurea (Emery)

*Ectatomma impressum* var. *purpureum* Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, (2)5: 444, worker, queen. Type locality: Hatam, Arfak Mts., Neth. New Guinea.

*Rhytidoponera* (*Chalcoponera*) *impressa* subsp. *purpurea,* Emery, 1910, Genera Insectorum, 118: 39.

*Rhytidoponera* (*Chalcoponera*) *impressa* var. *purpurea,* Viehmeyer, 1914, Deutsch. Ent. Z., p. 515.

*Rhytidoponera purpurea,* Brown, 1954, Breviora, Mus. Comp. Zool., no. 33: 7, worker, distrib.

*Material examined.* N-E. NEW GUINEA: Boana, Bunbok Valley, 1100 m. (Wilson, no. 1115); Nganduo, 1000 m. (Wilson, no. 735); Zingzingu, 1000 m. (Wilson, no. 768); Gemeheng, 1300 m. (Wilson, no. 786); Bulolo, 1025 m. (E. J. Ford, Jr.). This species also occurs on the Atherton Tableland of Queensland.

*Taxonomic note.* W. L. Brown (pers. commun.) has called my attention to the following differences between the North Queensland (Kuranda) and New Guinea samples. Workers of the two samples in the Museum of Comparative Zoology show approximately the same maximum size range, but those from Queensland average smaller. In living and freshly mounted specimens the metallic reflections of the head and alitrunk of the Queensland workers are predominantly reddish-purple, as opposed to bluish-purple in the New Guinea workers, and they are more extensive. These differences are relatively minor, however, and there seems to be no reason at present to dispute Brown's (1954) assignment of the Queensland series to *purpurea.*

*Ecological notes.* The author's New Guinea collections were all made in clearings and second-growth forest in the mountains of the Huon Peninsula. *R. purpurea* appears to be primarily arboreal in this area. At Nganduo a large colony was found nesting in the humus collected about the roots of an epiphytic fern lodged about two meters from the ground in the primary fork of a young tree. At Zingzingu and Boana, workers were found during the day foraging on the sides of trees. In North Queensland, on the other hand, Brown (1954) found this species nesting primarily in and under rotting logs on the ground in disturbed rain forest, although one nest-founding queen was discovered at the base of an epiphytic fern, well off the ground.

### Rhytidoponera rotundiceps Viehmeyer

*Rhytidoponera* (*Rhytidoponera*) *rotundiceps* Viehmeyer, 1913, Arch. Naturgesch., 79A(12): 28, fig. 2, worker. Type locality: Sattelberg, N-E. New Guinea.

*Material examined.* N-E. NEW GUINEA: Maroruo (near Sattelberg), 900 m. (Wilson, no. 729); Kua River Valley near Zengaru, 800 m. (Wilson, no. 796); Wamuki, 800 m. (Wilson, 850); Sambeang, 400 m. (Wilson, 864); Butala (Wilson, no. 867). All of the above localities, as well as the type locality Sattelberg, are within the adjacent watersheds of the Mongi and Mape Rivers on the Huon Peninsula. Butala is a coastal village at the mouth of the Mongi River.

*Ecological note.* All of the accessions listed above consisted of workers collected as strays on the floor of open, disturbed rain forest. Most were encountered during the day, but the collection at Maroruo was made during the early night.

### Rhytidoponera strigosa (Emery)

*Ectatomma araneoides* var. *strigosum* Emery, 1887, Ann. Mus. Civ. Stor Nat. Genova, (2)5: 444, worker. Type locality: Andai, near Manokwari, Neth. New Guinea. (Syntype examined — Emery Coll.) Viehmeyer, 1914, Deutsch. Ent. Z., p. 515, variability of worker petiole. Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)10: 437-438, male, doubtfully associated.

*Rhytidoponera* (*Rhytidoponera*) *strigosa*, Emery, 1910, Genera Insectorum, 118: 3.

*Rhitidoponera* [!] *subcyanea* subsp. *intricata* Emery, 1910, Nova Guinea, 5: 533, worker. Original localities: Manikion, Moaif, and Tawarin, Neth. New Guinea. (Syntype examined — Emery Coll.). NEW SYNONYMY.

*Rhytidoponera strigosa* var. *curvata* Stitz, 1912, Sitzber. Ges. Naturf. Freunde Berlin, p. 499, fig. 3, worker. Type locality: New Guinea (ex Kaiserin-Augusta-Fluss Exped.). (Syntypes examined — Zoologisches Museum, Berlin.) NEW SYNONYMY.

*Rhytidoponera schlaginhaufeni* Viehmeyer, 1912, Abh. Zool.-anthrop.-ethn. Mus. Dresden, 14: 4, fig. 2, worker. Type locality: Torricelli Mts., N-E. New Guinea. NEW SYNONYMY (provisional).

*Rhytidoponera nitens* Donisthorpe, 1949, Ann. Mag. Nat. Hist. (12)2: 403-405, worker, male. Type locality: Finschhafen, N-E. New Guinea (*nec* Maffin Bay, Neth. New Guinea, as stated in the original description; see discussion below). (Holotype examined — CAS.) NEW SYNONYMY.

*Material examined.* N-E. NEW GUINEA: Mt. Misim (H. Stevens); Bialowat (Stevens); lower Busu River (Wilson, nos. 708, 882, 951, 993, 1011); Bubia (Wilson, nos. 1067, 1074); Bandong, Bunbok Valley, 1300 m. (Wilson, no. 1124); Finschhafen (E. S. Ross); Sattelberg, 660 m. (Wilson, no. 772); Sattelberg-Maroruo, 900 m. (Wilson, no. 724); Maroruo, 900 m. (Wilson, no. 729); Bolingbangeng, 900-1000 m. (Wilson); Nganduo, 1300 m. (Wilson, no. 739); Yumzain-Joangeng, 1300 m. (Wilson, no. 741); Zingzingu, 1200 m. (Wilson, no. 761); Zengaru, 1600 m. (Wilson, no. 792); Kua River to Laulaunung, 1000-1300 m. (Wilson, no. 797); Tumnang, 1500 m. (Wilson, no. 801); Ebabaang, 1300-1400 m. (Wilson, no. 828); Wamuki, 800 m. (Wilson, no. 847); Butala (Wilson, no. 867). PAPUA: Dobodura (P. J. Darlington). *R. strigosa* is by far the most abundant member of the genus in the mountains of the Huon Peninsula.

*Taxonomic notes.* The material listed above shows notable variation in size, petiolar node shape, and sculpturing. Probably the most extensive variation is exhibited by the pattern of striation on the second gastric tergite. At one extreme, there is on the tergital midline near the posterior border a center of concentricity around which a few semicircular striae are clustered; at several striae distance anterior to the center the striae flatten out, and cross the entire tergite transversely, showing only slight posterior curving. At the other extreme of variation, the center

of concentricity is located on the tergital midline a short distance behind the anterior tergital border; those striae located the farthest anterior to the center are nearly semicircular, those farther back curve posteriorly more sharply and form parabolas, while those at or very near the center itself run posteriorly in a nearly straight line parallel to the midline of the tergite and extend back all the way to the posterior tergital border. Various degrees of intermediacy between these two extreme patterns occur in the material studied.

Worker head width ranges from 1.54 mm (Busu River, acc. no. 951) to 2.10 mm (Busu River, acc. no. 993). The petiolar node varies slightly in thickness and in the sharpness of the dorsal truncation. Series from Sattelberg and Nganduo are exceptional in showing feeble bluish surface reflections on the gaster; these specimens are otherwise identical to completely non-metallescent *strigosa* from nearby localities. A single specimen from Dobodura deviates in having very coarse striae on the first gastric tergite and in the non-concentric pattern of these striae, which originate at the anterior tergital border and diverge obliquely from the midline.

More material and a careful analysis of variation is much needed in the case of *R. strigosa*. There is a chance that further study will reveal the presence of two or more sibling species which the author has here provisionally grouped under this single species.

A special note concerning the synonym *R. nitens* Donisthorpe is required here. The collection data cited by Donisthorpe for the type series ("Maffin Bay, Dutch New Guinea, May 5th and September, 1944. E. S. Ross Coll.") is evidently at least partly in error. Through the courtesy of Dr. Ross I have been able to examine the entire type series of *nitens*, and this has proved to consist of a specimen labeled as the holotype along with a connidal worker paratype series from Finschhafen (May 10, 1944; E. S. Ross), as well as a single paratype male from Maffin Bay (September, 1944; Ross). Finschhafen must be considered the correct type locality. The holotype nest series falls well within my present conception of *R. strigosa*.

*Ecological notes.* On the Huon Peninsula this species is relatively abundant all the way from near sea level to 1500 meters.

Like the closely related *R. laciniosa*, it is primarily a rain forest dweller, although at the upper limits of its elevational range it occurs principally in clearings and open second-growth forest. Workers were commonly found foraging on the ground during the day, occasionally climbing onto rotting stumps and low herbaceous and shrubby vegetation. At Maroruo the foraging was found to extend into at least the early part of the night. The prey of *strigosa* workers generally consists of small insects; specific prey recorded at the Busu River included a moth larva, a meliponid bee, and a small scolytid beetle. The actual capture of the scolytid was observed. The *strigosa* worker seized this insect with its mandibles immediately upon making contact, lifted it from the ground, manipulated it for a moment with the help of its fore tarsi, and then carried it off homeward. The scolytid was too small to offer much resistance, and the ant made no attempt to use its sting.

Only a single nest of this species was found. This was near Zengaru, at the highest elevation recorded for *strigosa*. The nest was marked by a single large entrance gallery, about 7 cm. in diameter, leading horizontally into the clay embankment of a native trail in second-growth forest.

### Rhytidoponera subcyanea Emery

*Rhytidoponera subcyanea* Emery, 1897, Ann. Mus. Civ. Stor. Nat. Genova, 38: 548, worker. Type locality: Moroka, Papua. (Syntype examined — Emery Coll.)

*Rhytidoponera subcyanea* subsp. *transversiruga* Emery, 1910, Nova Guinea, 5: 532-533, worker. Original localities: Cyclops Mts. and Manikion, Neth. New Guinea. (Syntype examined — Emery Coll.) NEW SYNONYMY (provisional).

*Rhytidoponera subcyanea* var. *aruana* Karawajew, 1925, Konowia, 4: 78, worker. Type locality: Kobror I., Aru Archipelago. NEW SYNONYMY (provisional).

*Rhytidoponera wallacei* Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 474, worker. Type locality: Aru. NEW SYNONYMY (provisional).

A syntype of *transversiruga* in the Emery Collection differs from a syntype of *subcyanea* in the same collection in having the rugae of the occiput, alitrunk, and first gastric tergite more pronounced and tending less to form a reticulum. It may eventually prove to be a distinct species. According to the

original description, Karawajew's var. *aruana* differs from the "typical" *subcyanea* (as characterized by Emery; Karawajew did not have specimens at hand) only by minor sculptural and color characters. In his description of *wallacei*, Donisthorpe does not give any indication that he was aware of either *subcyanea* or *aruana*, and no characters are mentioned which can be used to separate his species from either of these two forms.

## IV. THE TRIBE PONERINI[1]

### Ponera Latreille

The *tenuis* and *selenophora* groups, comprising nearly 50 per cent of all the Melanesian species of *Ponera*, have been dealt with in full in an earlier revision.[2] In the present paper attention is devoted to the other species of *Ponera*, with emphasis on those undescribed or inadequately treated in the previous literature.

The zoogeographic pattern shown by *Ponera* is similar to that described for *Leptogenys* in an earlier paper.[3] Western Melanesia, and in particular New Guinea, contains a rich mixture of groups that are precinctive or at least Papuan-centered. The Fiji Islands contain five endemic species closely allied to common western Melanesian species, and their coverage here separate from the fauna of western Melanesia is principally a matter of taxonomic convenience rather than a real zoogeographic division. New Caledonia has two distinct endemic species, both closely allied to species occurring in North Queensland. Also occurring in Melanesia are two forms, *P. gleadowi* Forel and *P. perkinsi* Emery, which range widely through the Pacific region as tramp species. *P. perkinsi* is a member of the Papuan-based *biroi* group, being most closely allied to *biroi* itself, and may have its endemic

[1] Exclusive of *Myopias* (= *Trapeziopelta*), currently being revised by R. B. Willey and W. L. Brown. The ponerine genus *Pseudoponera* has been erroneously recorded from Melanesia by Donisthorpe; his *P. lubbocki* has recently been shown to be a synonym of *Leptogenys breviceps* Viehmeyer (Wilson, 1958, Bull. Mus. Comp. Zool. 118:116).

[2] Wilson, E. O. 1957. The *tenuis* and *selenophora* groups of the ant genus *Ponera*. Bull. Mus. Comp. Zool., 116: 355-386.

[3] Bull. Mus. Comp. Zool., 118: 101-142, 1958.

center somewhere in Melanesia. The origin of *P. gleadowi* is unknown; there is no evidence to indicate that it is endemic to any part of its present range in the Pacific.

## The Species of Western Melanesia and the Moluccas

*Ponera* in this region gives the impression of being at an early stage of evolutionary expansion, in that it consists almost entirely of groups of closely related species, several of which show exceptional amounts of intraspecific variation. Furthermore, the species groups themselves are poorly demarcated, with morphologically intermediate species such as *clavicornis, pruinosa,* and *papuana* making clean division difficult or impossible. Below is offered a tentative arrangement of species groups arrived at in the present study, along with a list of newly established synonymy at the species level.

### Group of *P. biroi* Emery

*biroi* Emery
*macradelphe* Wilson
*punctiventris* Emery
*sororcula* Wilson

### Group of *P. confinis* Roger

*confinis* Roger
*pallidula* Emery
=*Ponera pallidula* var. *fuscula* Emery

### Group of *P. gleadowi* Forel

*gleadowi* Forel
=*Ponera gleadowi* r. *decipiens* Forel
=*Ponera kalakauae* Forel
=*Ponera mina* Wheeler
=*Ponera mumfordi* Wheeler

### Group of *P. papuana* Emery

*papuana* Emery

Group of *P. pruinosa* Emery

*pruinosa* Emery
=*Ponera mocsaryi* Emery
*sabronae* Donisthorpe

Group of *P. selenophora* Emery

*clavicornis* Emery
*elegantula* Wilson
*selenophora* Emery
*syscena* Wilson
*xenagos* Wilson

Group of *P. tenella* Emery

*tenella* Emery

Group of *P. tenuis* Emery

*huonica* Wilson
*petila* Wilson
*ratardorum* Wilson
*szaboi* Wilson
*szentivanyi* Wilson
*tenuis* (Emery)

Incertae Sedis

*emeryi* Donisthorpe
*pia* Forel
*siremps* Forel

Species Newly Excluded from *Ponera*

*anommata* Donisthorpe (=*Cryptopone testacea* Emery)
*bicolor* Donisthorpe (=*Brachyponera croceicornis* Emery)
*caeca* Donisthorpe (=*Proceratium papuanum* Emery)

## *Key to the species, based on the worker caste*[1]

1. Eyes completely lacking; small light brownish to clear yellow species 2
   Eyes present, although often containing only a single ommatidium and very inconspicuous; size and color varying among species ..... 4
2. (Based on original description.) Antennal scapes reaching the occipital border; 3-4 irregularly shaped teeth present on the masticatory border of the mandible posterior to a set of 3-4 distinct, regularly shaped apical teeth (New Britain) ..... *siremps* Forel
   Antennal scapes failing to reach the occipital border at any point; masticatory border of mandible bearing only minute denticles behind the set of three apical teeth (species known only from Hawaii; possibly introduced by man from Melanesia) ..... 3
3. Larger species, head width at least 0.44 mm; cephalic index at least 81; erect hairs numerous on scape, dorsum of alitrunk, and entire surfaces of first two gastric tergites ..... *zwaluwenburgi* (Wheeler)
   Smaller species, head width not exceeding 0.30 mm; cephalic index not more than 78; erect hairs absent from scapes, alitruncal dorsum, and all but the posterior strips of the first two gastric tergites ..... *swezeyi* (Wheeler)
4. Showing the following combination of characters: relatively small species (HW 0.43-0.48 mm) with proportionately broad petiolar node, the dorsal width of which is at least 0.76X the pronotal width; genae coarsely punctate and completely opaque ..... 5
   Not showing all of the above characters; either well outside the given size range, or else the petiolar node is proportionately much narrower, or the genae are shallowly punctate and feebly shining, or a combination of these exceptions is shown ..... 6
5. Dorsal surface of alitrunk covered by abundant, short, erect to oblique hairs; dorsal petiolar node width only about 0.77-0.78X the pronotal width ..... *papuana* Emery
   Dorsal surface of alitrunk completely devoid of standing pilosity; dorsal petiolar node width at least 0.83X the pronotal width ..... *clavicornis* Emery
6. Smaller species, head width not exceeding 0.44 mm and usually much less ..... 7
   Larger species, head width never less than 0.49 mm and usually much more ..... 13

[1] Exclusive of *P. emeryi* Donisthorpe and *P. pia* Forel, both of which are *species inquirendae* described from sexual forms. Included are two Hawaiian species, *P. swezeyi* (Wheeler) and *P. zwaluwenburgi* (Wheeler), which may have faunal origins in Melanesia.

7. Petiolar node short, its length (measured from the side) not exceeding 0.11 mm; seen from above, its dorsal surface more than three times broader than long; subpetiolar process lobose and projecting anteriorly ..... *pallidula* Emery

   Petiolar node longer, its length at least 0.13 mm; seen from above, its dorsal surface not more than twice as broad as long; subpetiolar process angular or subangular and projecting posteriorly ..... 8

8. Very small species, head width not exceeding 0.31 mm; petiolar node seen from directly above, so that the posterior face is level with the line of vision, forming distinctly more than a half-circle, its width 0.15 mm or less ..... *szaboi* Wilson

   Larger species, head width never less than 0.32 mm and often as much as 0.38 mm; petiolar node seen from above varying among species, from distinctly more than semicircular to distinctly less, its width never less than 0.18 mm ..... 9

9. Antennal club indistinctly 5-jointed; petiolar node seen from directly above forming distinctly less than a half-circle ... *ratardorum* Wilson

   Antennal club distinctly 4-jointed; petiolar node seen from directly above forming a half-circle or more ..... 10

10. Smaller species, head width 0.34 mm or less; body color clear yellow to yellowish brown ..... 11

    Larger species, head width 0.38 mm or more; body color varying among species, from light yellowish brown to dark brown ..... 12

11. Lateral surfaces of alitrunk very feebly shagreened to smooth, and shining; petiolar node relatively low, its height (measured from the level of the lowermost point of the subpetiolar process to the level of the dorsal crest) only 0.25 mm, or about the same as the pronotal width ..... *petila* Wilson

    Lateral surfaces of alitrunk all moderately shagreened, and opaque; petiolar node proportionately higher, and its height in the single type specimen that can be measured is 0.29 mm, or slightly more than the pronotal width, which is 0.27 mm ..... *szentivanyi* Wilson

12. Petiolar node seen from directly above forming distinctly more than a half-circle; posterior apex of subpetiolar process sharply truncated; slightly smaller species, head width 0.40-0.41 mm; head dark brown, remainder of body medium brown ..... *huonica* Wilson

    Petiolar node seen from directly above forming almost an exact half-circle; posterior apex of subpetiolar process not truncated, but forming a full right angle or acute angle; slightly larger species, head width 0.42-0.44 mm; entire body uniformly dark brown ..... *tenuis* (Emery)

13. Showing the following combination of characters: dorsal petiolar node width at least 0.77X the pronotal width; seen from directly above,

the dorsal surface of the node is crescentic or arcuate, the strongly convex anterior border curving back to meet the straight or concave posterior border, with the juncture of the two borders angulate or subangulate ..... 14

Showing one or both of the following opposing characters: the dorsal petiolar node is 0.72X the pronotal width or less; or the dorsal surface of the node seen from directly above is elliptical or lenticular, with the posterior border nearly as convex as the anterior, and the two borders merging laterally without any sign of an angle of juncture 17

14. Head more elongate (cephalic index 80), with relatively large eyes containing 11 or 12 ommatidia; alitrunk completely devoid of standing hairs ..... *elegantula* Wilson

Head proportionately shorter (cephalic index 86 or more), with smaller eyes containing only 3-5 indistinct ommatidia; alitrunk covered with abundant standing hairs ..... 15

15. Smaller species, head width of unique type 0.52 mm; posterior face of petiolar node feebly but distinctly convex; anterior surface of scape bearing abundant erect hairs ..... *syscena* Wilson

Larger species, head width not less than 0.59 mm; posterior face of petiolar node either flat or feebly concave; anterior surface of scape with few or no standing hairs ..... 16

16. Smaller species, head width 0.59-0.63 mm; basal half of masticatory border of mandible bearing two distinct teeth which are nearly as large as the three teeth of the apical half; posterior border of petiolar node seen from directly above distinctly concave ..*selenophora* Emery

Larger species, head width 0.65-0.68 mm; basal half of masticatory border of mandible bearing only minute denticles which do not approach in size the three apical teeth; posterior border of petiolar node seen from directly above almost perfectly straight ..... *xenagos* Wilson

17. Cephalic index 75 in single syntype measured; an exceptionally slender, blackish brown species of medium size for *Ponera* (head width 0.53 mm) ..... *tenella* Emery

Cephalic index never less than 78, ranging below 80 only in the species *sororcula* Wilson, which is slightly smaller than *tenella* (head width 0.44-0.52 mm) and yellowish brown in color ..... 18

18. Body color blackish brown to jet black. Showing in addition the following combination of characters: medium to large in size, head width 0.53-0.88 mm; petiolar node seen from the front broadly ovate, seen from the side thin and tapering and more or less symmetrical; genae and thoracic dorsum shallowly punctate and feebly shining; eye containing at least five ommatidia ..... 19

Body color brownish yellow to medium brown. Not showing all of the above additional characters ..... 20

19. Smaller species, head width 0.53-069 mm ..... *pruinosa* Emery
Larger species, head width 0.73-0.88 mm ..... *sabronae* Donisthorpe

20. Showing the following combination of characters: medium-sized, maximum head width range 0.44-0.62 mm; when head is viewed in full face and the scapes are aligned flat against the head and parallel to its long axis, the scapes surpass the occipital border by only their maximum width or less; color brownish yellow to light reddish brown . 21
Not showing all of the above characters ..... 22

21. Larger species, head width 0.55-0.62 mm; dorsal surface of head posterior to clypeus coarsely and densely punctate, and completely opaque ..... *punctiventris* Emery
Smaller species, head width 0.46-0.52 mm; dorsal surface of head posterior to clypeus more finely punctate, and subopaque to feebly shining ..... *sororcula* Wilson

22. Most of dorsal head surface posterior to clypeus coarsely punctate or shagreened, and opaque; petiolar node in side view subrectangular, its anterior and posterior borders nearly parallel ..... 23
Most of dorsal head surface posterior to clypeus weakly sculptured and feebly shining; petiolar node in side view subtrapezoidal, tapering markedly toward the dorsal border ..... 24

23. Eyes minute, containing only one to three ommatidia, their maximum length 0.03 mm or less; scape index 80-86; occipital margin seen in full face view strongly concave (New Guinea to Solomons) ... *biroi* Emery
Eyes larger, containing at least five or six ommatidia, their maximum length 0.04 mm or more; occipital margin seen in full face view feebly concave (widespread in Pacific region, known from New Caledonia, and possibly as tramp species or even endemic in western Melanesia) ..... *perkinsi* Forel

24. Larger species, head width 0.64-0.66 mm. Showing in addition the following combination of characters: scapes slightly exceed occipital border when held flat against the head and aligned with the long axis of the head; entire alitruncal surface smooth and shining; body color light reddish brown ..... *macradelphe* Wilson
Smaller species, head width not exceeding 0.52 mm. Not showing all of the additional characters listed above ..... 25

25. Maximum eye length less than 0.03 mm; body color light yellowish brown, head occasionally approaching medium brown; petiolar node height 0.22-0.26 mm, rarely exceeding 0.25 mm ..... *gleadowi* Forel
Maximum eye length exceeding 0.03 mm, if only by a very small amount; body color uniformly medium brown; petiolar node height 0.26-0.28 mm. ..... *confinis* Roger

### Ponera biroi Emery

*Ponera Birói* Emery, 1900, Természetr. Füz., 23: 318, pl. 8, fig. 9, worker, queen. Type locality: Friedrich-Wilhelmshafen (= Madang), N-E. New Guinea. (Metatype examined — Hungarian National Museum).

*Material examined.* NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N-E. NEW GUINEA: Bubia (Wilson, nos. 679, 689); lower Busu River (Wilson, nos. 964, 966, 1042); Sattelberg (metatype; L. Biró); valley of Kua River, near Zengaru, 800 m. (single dealate queen; Wilson, no. 795). NEW BRITAIN: St. Paul's, 350 m., Bainings Mts., Gazelle Pen. (J. L. Gressitt). SOLOMONS: Fulakora, Santa Isabel (W. M. Mann).

*Taxonomic note.* Workers from Maffin Bay (Neth. N. G.), New Britain, and the Solomons differ from those from N-E. New Guinea in having more weakly sculptured petiolar nodes. The nodes of the Maffin Bay workers are in addition thinner in side view and with slightly less convex anterior faces than in material from other localities.

*Ecological notes.* At Bubia and the Busu River, colonies of this species were found nesting in small "passalid-stage" logs on the rain forest floor. A colony collected entire at the Busu River contained a single nest queen, about 25 workers, and 20 to 30 larvae, all one-quarter to half grown. Occasional foraging workers were taken in the Busu River forest by knocking off material from the undersurface of small rotting logs.

### Ponera clavicornis Emery

*Ponera clavicornis* Emery, 1900, Természetr. Füz., 23: 317, pl. 8, figs. 7, 8, worker. Type locality: Friedrich-Wilhelmshafen (= Madang), N-E. New Guinea. Wilson, 1957, Bull. Mus. Comp. Zool., 116: 377-379, worker, dist., ecology. (Syntype examined — Emery Coll.)

*Selenopone clavicornis*, Wheeler, 1933, Amer. Mus. Novitates, no. 672: 22.

### Ponera confinis Roger

*Ponera confinis* Roger, 1860, Berl. Ent. Z., 4: 284, worker. Type locality: Ceylon. Forel, 1901, Mitt. Zool. Mus. Berl., 2: 8, dist. Emery, 1911, Genera Insectorum, 118: 90, dist. Stitz, 1911, Sitzber. Ges. Nat. Freunde Berl., p. 356, dist.

*Material examined.* PAPUA: Karema (Wilson, no. 599); Bisianumu, 500 m. (Wilson, nos. 635, 642). NEW HEBRIDES: Ounua, Malekula (L. E. Cheesman). Emery (1911) records this species from India, Ceylon, Burma, and Sumatra. Forel (1901) found it in the Dahl collection from New Britain, and Stitz (1911) records it from N-E. New Guinea.

*Taxonomic note.* In the present study I have followed Emery's conception of this species, as indicated by determined series in his personal collection.

*Ecological note.* At Bisianumu two colonies of *confinis,* both containing less than 50 workers, were found nesting in small rotting logs on the rain forest floor. According to Forel (1901), Dahl collected this species in New Britain in both rain forest and a cultivated (cotton) field.

### Ponera elegantula Wilson

*Ponera elegantula* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 379-381, worker, queen. Type locality: Tumnang, 1500 m.; Huon Pen., N-E. New Guinea.

### Ponera emeryi Donisthorpe, emend.

*Ponera emergi* [!] Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)10: 443, male. Type locality: Camp Nok, 800 m., Waigeo.

The unique type of *emeryi* was not available during the course of the present study. Donisthorpe's brief description is virtually useless for comparative purposes, and in view of the fact that he commonly placed isolated males, as well as entire nest series, in the wrong genus and tribe, there can be no assurance that *emeryi* even belongs in *Ponera.*

### Ponera gleadowi Forel

*Ponera Gleadowi* Forel, 1895, Mem. R. Accad. Sci. Bologna, (5)5: 292-293, nota, figs. 17a-c, worker. Original localities: Poona, Orissa, and Thana, India. Mann, 1919, Bull. Mus. Comp. Zool., 63: 294, dist. (Syntype examined — Emery Coll.).

*Ponera kalakauae* Forel, 1899, Fauna Hawaiiensis (Cambridge), pp. 116-117, worker, queen. Type locality: Lihue, Kauai, Hawaii. NEW SYNONYMY (provisional).

*Ponera gleadowii* r. *decipiens* Forel, 1899, *ibid.*, p. 118, worker. Type locality: Kauai (coast), Hawaii. NEW SYNONYMY (provisional).

*Ponera mina* Wheeler, 1927, Proc. Amer. Acad. Arts Sci., 62: 131-134, fig. 2, worker, queen, male. Type locality: Norfolk Island. (Syntypes examined — MCZ). NEW SYNONYMY (provisional).

*Ponera mumfordi* Wheeler, 1933, Bull. Bishop Mus., no. 114: 141-142, worker. Type locality: summit of Kohepu, Uapou, Marquesas. (Syntypes examined — MCZ.) NEW SYNONYMY (provisional).

*Material examined.* NETH. NEW GUINEA: Maffin Bay (winged queen, October, 1944; E. S. Ross). N-E. NEW GUINEA: Finschhafen (Ross). NEW HEBRIDES: Tanna (L. E. Cheesman). FIJI ISLANDS: Nadarivatu (W. M. Mann). NEW CALEDONIA: 11 km. southeast of La Foa (C. L. Remington); "S. E. New Caledonia" (N. L. H. Krauss); Ciu, 300 m. (Wilson, no. 297). Mann (1919) has recorded this species from Pamua, San Cristoval, Solomons.

*Taxonomic notes.* The status of the species of the *gleadowi* complex has been one of the most perplexing problems in the taxonomy of the Melanesian ant fauna. In analyzing this complex, I started with the working hypothesis that there are at least two species in the Indo-Australian area, the most divergent forms corresponding to *gleadowi* (with race *decipiens*) and *mumfordi*, respectively. Eighteen nest series from this area were studied, and the following characters were examined in detail: head shape, antennal length, mandible form, mandibular dentition, alitrunk form, petiole form, sculpturing, pilosity, and color. Particular attention was paid to petiole form, which has been utilized extensively by past authors and seemed to offer the most promising diagnostic variation. In none of the characters, or any combination of them, could a division be made. In particular, the *gleadowi* variant (represented by a worker from Colombo, Ceylon, compared with a *gleadowi* syntype) and *mumfordi* variant are connected by graded intermediate forms, with several New Caledonian series being the most centrally located. It was concluded that all of the study series are conspecific. This decision and the resultant synonymy should be considered provisional, however, until a more thorough study can be undertaken, utilizing longer series and additional characters. The fact that in the *gleadowi* group as a whole and in other groups of

*Ponera* such poorly understood characters as palpal segmentation and male ergatomorphism are occasionally of species-diagnostic value should be more than sufficient reason to use caution.

*Ecological note.* At Ciu, New Caledonia, a small colony of *gleadowi* was found nesting in a rotting log in moist subtropical evergreen forest.

### Ponera huonica Wilson

*Ponera huonica* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 365-367, fig. 2, worker, queen, male. Type locality: Ebabaang, Huon Pen., N-E, New Guinea.

### Ponera macradelphe Wilson, n. sp.

*Diagnosis.* A member of the *biroi* group easily distinguished from other members of the group by the combination of large size, small, single-facet eyes, smooth and shining alitruncal dorsum, and light ferruginous color. Its closest affinities are to *punctiventris* Emery and *sororcula* Wilson.

*Holotype worker.* HW 0.65 mm, HL 0.80 mm, SL 0.59 mm, CI 81, SI 91, PW 0.52 mm, dorsal petiole width 0.36 mm, petiolar node length 0.24 mm, petiolar node height 0.40 mm. The apical quarter of the masticatory border of the mandible occupied by four teeth, the basalmost of which is very low and rounded and inconspicuous. The basal three-quarters of the border occupied by an even series of minute denticles. Eye small, consisting of a single ommatidium, located approximately 0.75 the distance from the lateral occipital border to the midpoint of the anterior clypeal border. Antenna lacking a well defined club, the terminal six segments gradually increasing in size distally. The median portion of the clypeus prominently raised, but lacking a distinct longitudinal carina. Anterior clypeal border in full-face view evenly convex, lacking any sign of a central projection or angulation. Head in full-face view distinctly narrowed anteriorly; posterior half of lateral cephalic borders convex, anterior half feebly but distinctly concave (in *punctiventris* and *sororcula* the entire lateral border is gently convex); posterior cephalic border moderately concave. Alitrunk in side view

flattened as a whole, the pronotum and mesonotum each individually very feebly convex, the dorsal propodeal border almost perfectly straight. The promesonotal suture and metanotal zone are each marked by very faint impressions. Petiolar node seen from the side gently tapering dorsally, with straight anterior and moderately convex posterior borders, and broadly and evenly rounded, strongly convex dorsal surface. Seen from directly above, so that the posterior face is exactly even with the line of vision, the dorsal surface of the node is roughly lenticular in shape, with moderately convex (and poorly demarcated) anterior border, broad, moderately convex lateral borders, and very feebly convex, nearly straight posterior border. Subpetiolar process lobose and directed anteriorly.

Frontal lobes, and frontal area as far as 0.12 mm posterior to the posteriormost tip of the frontal carinae, shagreened and subopaque. Remainder of head, including mandibles and clypeus, very feebly shagreened to perfectly smooth, and feebly to moderately shining. Entire dorsal surface of alitrunk very feebly shagreened to smooth, and moderately shining, except for limited areas in the upper posterior section of the mesepisternum and around the metapleural gland, which are more strongly shagreened and subopaque. All of petiolar node surface feebly shagreened to smooth, and moderately shining, except the ventral third of the lateral face, which is more strongly shagreened and subopaque. First gastric tergite densely punctate-shagreened, and almost entirely subopaque; second tergite more feebly punctate-shagreened, and feebly shining over most of its surface.

Oblique to erect pilosity of variable length abundant over all body and appendage surfaces, except anterior and posterior faces of petiolar node and anterior declivity of gaster, which are bare. All of body and appendages covered in addition by abundant, predominantly appressed pubescence.

Entire body light ferruginous, the gaster a shade darker and the appendages a shade lighter than the remainder of the body.

*Worker paratypes.* HW 0.64-0.66 mm, HL 0.82 mm, SL 0.59-0.60 mm, CI 78-80, SI 91-92, PW 0.52-0.54 mm, dorsal petiole width 0.37-0.38 mm, petiolar node length 0.25 mm.

*Material examined.* N-E. NEW GUINEA: Ebabaang, 1300-1400 m., Huon Pen., holotype and two paratype workers (Wilson, no. 839).

*Ecological note.* The three type workers were taken close together in thick leaf litter and humus on the floor of dense mid-mountain rain forest.

### Ponera pallidula Emery

*Ponera pallidula* Emery, 1900, Természetr. Füz., 23: 320-321, worker. Type locality: Friedrich-Wilhelmshafen (= Madang), N-E. New Guinea. *Nec* Mann, 1919, Bull. Mus. Comp. Zool., 63: 295. *Nec* Wheeler, 1927, Proc. Amer. Acad. Arts Sci., 62: 129-130. (Syntypes examined — Hungarian National Museum).

*Ponera pallidula* var. *fuscula* Emery, 1902, Természetr. Füz., 25: 158, worker, queen. Type locality: Sattelberg, N-E. New Guinea. NEW SYNONYMY.

*Material examined.* N-E. NEW GUINEA: Madang (syntypes); lower Busu River (Wilson, nos. 884, 1052, 1058); Zingzingu, 1000 m. (Wilson, no. 770). PAPUA: Bisianumu, 500 m. (Wilson).

*Taxonomic notes.* Workers collected by the author in eastern New Guinea appear to be identical to the *pallidula* syntypes except for their darker body color, and they therefore probably correspond to Emery's var. *fuscula*. The *pallidula* types are uniformly brownish yellow (Emery described them as "flavo-testacea" in 1900), whereas my own specimens have medium brown bodies and brownish yellow appendages. It should be mentioned that Emery's figure of the *pallidula* worker shows the petiolar node somewhat thicker than is actually the case.

*Ecological note.* At the Busu River workers of this species were collected in soil-litter berlesates from the floor of primary rain forest.

### Ponera papuana Emery

*Ponera papuana* Emery, 1900, Természetr. Füz., 23: 319, pl. 8, figs. 10, 11, worker, queen. Type locality (by present selection): Mt. Hansemann, N-E. New Guinea. *Nec* Mann, 1919, Bull. Mus. Comp. Zool., 63: 295. (Syntypes examined — Hungarian National Museum; MCZ; see below.)

The following re-description of this problematic species is based on two syntype workers from Mt. Hansemann loaned to the author by Dr. Elisabetha Bajári of the Hungarian National Museum. With Dr. Bajári's permission, one of these specimens has been selected as lectotype and returned to the Hungarian National Museum, while the other has been retained in the Museum of Comparative Zoology.

*Lectotype worker.* HW 0.47 mm, HL 0.58 mm, SL 0.44 mm, CI 81, SI 94, PW 0.38 mm, dorsal petiole width 0.29 mm, petiolar node height 0.15 mm. Mandibular dentition consisting of a single rather small apical tooth followed by an irregular series of teeth varying in size from nearly as large as the apical tooth to barely visible (at 50X) denticles. Eye small, inconspicuous, consisting of a single ommatidium located about 0.75X the distance from the lateral occipital border to the midpoint of the anterior genal border. Median portion of the clypeus elevated but not forming a distinct longitudinal carina. Viewed in full face, the anterior clypeal border is moderately and evenly convex. Head subrectangular, distinctly narrower anterior to the eyes than at the occipital zone, its sides moderately convex; viewed in full face the posterior border is shallowly but distinctly concave. In side view the dorsal surface of the alitrunk is almost perfectly flat, with only very faint, barely visible depressions marking the promesonotal and mesonotal-propodeal junctures. Promesonotal suture seen from above well marked, the metanotal area undifferentiated. Petiolar node seen in side view appearing to curve forward slightly as a whole, its posterior border moderately convex, its anterior border almost perfectly straight. Seen from directly above, the node is proportionately wide, its width 0.77X the pronotal width; its dorsal surface lenticular in shape, with broad, rounded lateral margins.

Mandibles sparsely and feebly punctate, their surfaces strongly shining. Clypeus somewhat more densely punctate, its surface feebly shining. Remainder of head finely and densely punctate, and completely opaque. Entire remainder of body somewhat less densely punctate than the head exclusive of the mandibles, and subopaque.

Clypeus bearing several long, erect hairs. Short erect or oblique hairs present on mandibles, frontal lobes, anterior gular

surface, entire dorsal alitruncal surface, and entire surfaces of gastric tergites. Standing pilosity absent from most of dorsal head surface and petiolar node. Entire body and appendages covered by abundant, oblique to appressed pubescence.

Body uniformly dark reddish brown, appendages yellowish brown. Emery describes the type series when relatively freshly collected as "picea vel (immatura) ferrugineo-testacea, mandibulis, funiculo, trochanteribus, tibiis, tarsis anoque dilutius rufescentibus."

*Paratype worker.* HW 0.47 mm, HL 0.56 mm, SL 0.46 mm, CI 84, SI 98, PW 0.38 mm, dorsal petiolar width 0.29 mm. This specimen is almost identical to the lectotype in other external characters.

### Ponera perkinsi Forel

*Ponera perkinsi* Forel, 1899, Fauna Hawaiiensis (Cambridge), p. 117, worker, queen, male. Type locality: Hawaiian Islands, in mountains, 650-1300 m. (Syntype examined — Emery Coll.).

*Ponera Andréi* Emery, 1900, Természetr. Füz., 23: 318, nota, pl. 8, fig. 47, worker. Type locality: Nouméa, New Caledonia. (Holotype examined — Emery Coll.) NEW SYNONYMY.

The unique type of *P. andrei* was compared directly with a worker syntype of *P. perkinsi* in the Emery Collection and found to be nearly identical. *P. perkinsi* has not yet been recorded from northern and central Melanesia, although it has been recorded from New Caledonia and is widespread (as a tramp species?) in Polynesia. Some pains have been taken to diagnose it in the key because of the ease with which it can be confused with the closely related *P. biroi* Emery.

### Ponera petila Wilson

*Ponera petila* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 368, fig. 2, worker. Type locality: lower Busu River, Huon Pen., N-E. New Guinea.

### Ponera pia Forel

*Ponera Pia* Forel, 1901, Mitt. Zool. Mus. Berl., 2(1, b): 9, queen. Type locality: Ralum, New Britain.

### Ponera pruinosa Emery

*Ponera pruinosa* Emery, 1900, Természetr. Füz., 23: 319, pl. 8, figs. 13, 14, worker. Original localities: Tamara I., Huon Gulf, and Lemien, near Berlinhafen (= Aitape), N-E. New Guinea. Mann, 1919, Bull. Mus. Comp. Zool., 63: 294-295, queen, male, dist. (Syntype examined — Emery Coll.).

*Ponera Mocsáryi* Emery, 1900, *ibid.*, p. 320, pl. 8, figs. 15, 16, worker. Type locality: Tamara I., Huon Gulf, and Lemien, near Berlinhafen (= Aitape), N-E, New Guinea. NEW SYNONYMY (provisional).

*Material examined.* MOLUCCAS: Kalam I., Halmahera (C. S. Banks). NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N-E. NEW GUINEA: Nadzab (Wilson, nos. 1088, 1091); Didiman Creek, Lae (Wilson, no. 717); Bubia (Wilson, nos. 678, 681, 688, 1063, 1068, 1081); lower Busu River (Wilson, nos. 877, 884, 899, 1008, 1013); Finschhafen (N. G. L. Wagner, and Wilson, no. 718); Nganduo, 1000 m. (Wilson, nos. 734, 737); Zingzingu, 1000 m. (Wilson, no. 769); Kua River Valley, near Zengaru, 800 m. (Wilson, no. 793); Gemeheng, 1200-1300 m. (Wilson, nos. 776, 786); Wamuki, 800 m. (Wilson, no. 861). PAPUA: Karema, Brown River (Wilson, no. 580); Bisianumu, 500 m. (Wilson, no. 657). SOLOMON ISLANDS: Malapaina, Three Sisters (W. M. Mann); Wainoni Bay, San Cristoval (Mann); Pawa, Ugi (Mann); Auki, Malaita (Mann); Fulakora, Santa Isabel (Mann). NEW HEBRIDES: Ratard Plantation, near Luganville, Espiritu Santo (Wilson, nos. 319, 332, 347); Vanua Lava, Banks Group (L. E. Cheesman); Ounua, Malekula (Cheesman). I have also seen series of *pruinosa* from Camp Lookout, Cuernos Mts., Negros Oriental, Philippines, collected by J. W. Chapman.

*Taxonomic notes.* Emery characterized *P. mocsaryi* as follows: "[P. pruinosa Emery] simillima sed minor, capite angustiore, minus confertim punctata et parcius pubescens, vix pruinosa, oculis minoribus, stemmatibus 8-10 compositis, clypei carina antice obtusa, tamen marginem anticum medio subangulatum productum fere attingente, antennis minus crassis, thorace paulo gracilore, squama petioli minus crassa, superne magis attenuata. Caeterum *P. pruinosae* similis. — L. 2⅔-2¾ mm." Among the extensive New Guinea collections of *pruinosa* examined during the present study, occasional series show one or more of the

characters listed by Emery as distinguishing *mocsaryi*. At least one series (Kua Valley, accession no. 793) fits the description of *mocsaryi* in most of the characters, namely smaller size, proportionately smaller eyes, more slender body form, and less body pubescence. My first inclination was to treat this form as a distinct species, but examination of other series showed that it is connected to "typical" *pruinosa* by a gradient of intermediates. In addition to the *mocsaryi*-form trend, *pruinosa*, as broadly conceived at present, shows unusual variation in sculpturing (density of puncturation) and alitrunk form. In side view the alitrunk ranges from the "typical" *pruinosa* outline (as shown by the Emery Collection syntype), where the metanotal groove is deeply impressed and the mesonotum distinctly convex, to a much flattened dorsal outline of the sort exhibited by *P. papuana* Emery, where the metanotal groove is feebly impressed and the mesonotum almost flat. Future work may reveal that this exceptional variation encompasses two or more sibling species, but thus far I have been unsuccessful in detecting significant discontinuities in single characters or even consistent character combinations to mark species boundaries.

*Ecological notes. P. pruinosa* is among the most abundant and widespread of all Melanesian ants. Colonies have been taken over a wide elevational range, from near sea level to more than 1200 meters on the Huon Peninsula alone, and in a variety of forest types, from lowland and midmountain rain forest to dry, open riparian forest (at Nadzab). Colonies are generally small in size and nest almost exclusively in medium to large rotting logs. At Zingzingu, near the upper elevational limit of the species' distribution, a single colony (no. 769) was found nesting under a moss layer covering the base of a standing dead tree. Workers are commonly encountered foraging on the forest floor away from their nests, but even there usually remain hidden under covering objects such as pieces of rotting wood. The following note on predatory behavior was made at Bubia: when colonies of *Ponera pruinosa* and an undetermined species of termite nesting adjacently under the bark of a rotting log were exposed, the *Ponera* workers promptly attacked the termite colony and carried back to their own nest a quantity of the termite workers.

### Ponera punctiventris Emery

*Ponera punctiventris* Emery, 1902, Természetr. Füz., 25: 157-158, fig., worker. Type locality: Sattelberg, N-E. New Guinea. (Syntype examined — Emery Coll.)

*Material examined.* N-E. NEW GUINEA: Sattelberg (syntype); Nganduo, near Sattelberg, 1300 m. (Wilson, no. 739); Zingzingu, 1000 m. (Wilson, no. 771); Tumnang, 1500-1600 m. (Wilson, nos. 812, 834).

*Ecological note.* A small colony of *punctiventris,* containing winged queens, was collected at Tumnang during April 14-15, 1955 (acc. no. 812). It was nesting in the soil under a deep-set rock in midmountain rain forest.

### Ponera ratardorum Wilson

*Ponera ratardorum* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 369-370, figs. 1, 2, worker. Type locality: St. Paul's, Bainings Mts., New Britain.

### Ponera sabronae Donisthorpe

*Ponera sabronae* Donisthorpe, 1941, Ann Mag. Nat. Hist., (11)7: 130, worker, male. Type locality: Sabron, Cyclops Mts., Neth. New Guinea. (Syntype examined — MCZ.)

*Material examined.* NETH. NEW GUINEA: Sabron, Cyclops Mts. (syntype); Maffin Bay (E. S. Ross); Waghete, Tigi Lake, Wisselmeren, 1700 m. (J. L. Gressitt); Enarotadi, Wisselmeren, 1900 m. (Gressitt). N-E. NEW GUINEA: Joangeng, 1500 m. (Wilson, no. 745); Tumnang, 1500 m. (Wilson, no. 798).

*Taxonomic note.* The only character I have been able to find that separates *sabronae* from the sympatric *pruinosa* is the larger size of the former. A discontinuity in the joint samples of the two species exists (see key) despite the great size variability of *pruinosa.*

*Ecological notes.* At Joangeng a colony of *sabronae* was found nesting under the moss layer covering the upper surface of a large rotting log. At Tumnang stray workers were collected in leaf litter between the buttresses of a large tree at the edge of a clearing in mid-mountain rain forest.

### Ponera selenophora Emery

*Ponera selenophora* Emery, 1900, Természetr. Füz., 23: 317, pl. 8, figs. 4, 6, worker. Type locality: Lemien, near Berlinhafen (= Aitape), N-E. New Guinea. Wilson, 1957, Bull. Mus. Comp. Zool., 116: 382-384, fig. 3, worker, dist., ecology. (Syntype examined — Emery Coll.)
*Selenopone selenophora,* Wheeler, 1933, Amer. Mus. Novitates, no. 672: 21.

### Ponera siremps Forel

*Ponera siremps* Forel, 1901, Mitt. Zool. Mus. Berl., 2 (1, b): 8, worker. Type locality: vicinity of Ralum, New Britain.

### Ponera sororcula Wilson, n. sp.

*Ponera pallidula,* Mann, 1919, Bull. Mus. Comp. Zool., 63: 295. *Nec Ponera pallidula* Emery.

*Diagnosis.* A small, light-colored member of the *biroi* group with closest affinities to *punctiventris* Emery, from which it differs by its much smaller size, proportionately thinner and more flattened alitrunk, and feebler body sculpturing.

*Holotype worker.* HW 0.46 mm, HL 0.59 mm, SL 0.44 mm, CI 78, SI 96, PW 0.34 mm, dorsal petiole width 0.22 mm, petiolar node length 0.14 mm, petiolar node height 0.28 mm. Three apical teeth occupying about 0.6 of the masticatory border of the mandible, followed basally by an indeterminate number of serially arranged, minute denticles. Eye minute, consisting of a single ommatidium, located about 0.75X the distance from the lateral occipital border to the midpoint of the anterior genal border. Antenna lacking a differentiated club, the terminal six segments gradually increasing in size distally. Clypeus as described for *macradelphe* Wilson. Head seen in full face view slightly narrowed anteriorly, with moderately and evenly convex sides and moderately concave occipital border. Alitrunk as in *macradelphe,* except that the propodeal dorsum is feebly convex instead of straight in side view. Petiolar node in side view subrectangular, with straight anterior and feebly convex posterior faces and broad, feebly convex dorsal face. Seen from directly above, so that the posterior face is even with the line of vision, the anterior border of the node is strongly convex and merges into the nearly straight posterior border through an even curve. Subpetiolar process lobose and directed anteriorly.

Mandibles smooth and shining. Clypeus feebly shagreened and shining over most of its surface. Entire remainder of head densely but shallowly punctate, subopaque dorsally and feebly shining laterally. Entire dorsal and lateral alitrunkal surfaces feebly shagreened to smooth, and feebly to moderately shining, except for a limited area around the metapleural gland and the dorsal section of the lateral propodeal face, which are more strongly shagreened and subopaque. All but the posterior face of the petiolar node feebly shagreened, and feebly shining to subopaque. Gastric tergites densely punctate-shagreened, and subopaque.

Mandibles, clypeus, occiput, entire dorsal surface of alitrunk, dorsal and upper lateral surfaces of petiolar node, and entire gastric tergital surfaces (except anterior declivity of first tergite) bearing numerous oblique and erect hairs of variable length. Appendages almost entirely bare of standing pilosity. All of body and appendages covered by dense, predominantly appressed pubescence.

Body and appendages light ferruginous, the gaster a shade darker than the remainder of the body.

*Worker paratype variation.* NEW GUINEA: HW 0.46-0.52 mm, HL 0.57-0.63 mm, SL 0.42-0.45 mm, CI 79-83, SI 87-95, PW 0.33-0.40 mm, dorsal petiole width 0.23-0.29 mm, petiolar node length 0.14-0.16 mm, petiolar node height 0.26-0.30 mm. SOLOMON ISLANDS: HW 0.44-0.45 mm, HL 0.59 mm, SL 0.43-0.45 mm, CI 75-76, SI 98-100, PW 0.35-0.37 mm, dorsal petiole width 0.24-0.25 mm. As the data above show, the Solomon Islands workers have slightly more slender heads and a correspondingly higher scape index than those from New Guinea, but they are within the range of variation of the New Guinea samples in other characters. The single series comprising the largest workers examined (Didiman Creek, acc. no. 694; HW 0.51-0.52 mm) is unusual in that the appendages, including the scapes, bear a few scattered, short, erect hairs; this may be nothing more than a simple allometric development.

*Material examined.* N-E. NEW GUINEA: Didiman Creek, Lae, holotype worker (Wilson, no. 700) and three paratype workers (Wilson, nos. 694, 700); Nadzab, a single paratype worker (Wilson, no. 1110). SOLOMON ISLANDS: Auki, Malaita, 6 paratype workers (W. M. Mann).

*Ecological notes.* At Didiman Creek stray workers were found foraging during the day in leaf litter at the border of disturbed lowland rain forest. At Nadzab a single worker was collected in leaf litter in open, dry riparian forest.

### Ponera swezeyi (Wheeler)

*Pseudocryptopone swezeyi* Wheeler, 1933, Amer. Mus. Novitates, no. 672: 16-17, fig. 6, worker, queen. Type locality: vicinity of Honolulu, Hawaii. (Syntypes — MCZ.)

*Ponera swezeyi,* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 370-371, worker.

This species is known at present only from material collected in the vicinity of Honolulu, but as I have shown elsewhere (Wilson, 1957) there is an excellent chance that it was introduced there from a *tenuis*-group "source area" in Melanesia or the East Indies.

### Ponera syscena Wilson

*Ponera syscena* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 384-385, worker. Type locality: Yunzain-Joangeng, 1300 m., Huon Pen., N-E. New Guinea.

### Ponera szaboi Wilson

*Ponera szaboi* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 371-372, worker. Nom. pro *Cryptopone mocsáryi* Szabó, 1910, Rovartani Lap., 17: 186 (nec *Ponera moscaryi* Emery, 1900).

*Pseudocryptopone mocsaryi,* Wheeler, 1933, Amer. Mus. Novitates, no. 672: 14.

### Ponera szentivanyi Wilson

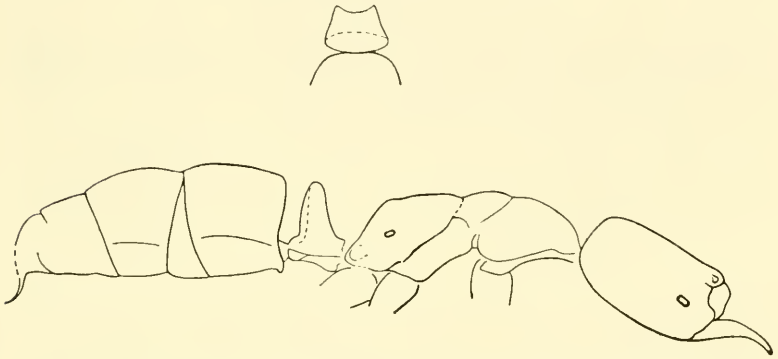
*Ponera szentivanyi* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 372-373, figs. 1, 2, worker. Type locality: Karema, Brown River, Papua.

### Ponera tenella Emery
### (Text-figure)

*Ponera tenella* Emery, 1902, Természetr. Füz., 25: 158-159, fig., worker, queen. Type locality: Sattelberg, N-E. New Guinea. (Syntype examined — Hungarian National Museum.)

The description below is based on a worker syntype loaned by Dr. E. Bajári of the Hungarian National Museum.

*Syntype worker.* HW 0.53 mm, HL 0.70 mm, SL 0.60 mm, CI 76, SI 113, PW 0.42 mm, dorsal petiole width 0.29 mm, petiolar node length 0.15 mm, petiolar node height 0.35 mm. Right mandible with three apical teeth occupying approximately one fourth of the masticatory border; posterior to these is an irregular series of teeth ranging in size from as large as the posterior two teeth of the apical set to barely visible denticles. Eye small but distinct, containing a single ommatidium, located approximately 0.8 the distance from the lateral occipital border to the



*Ponera tenella* Emery, syntype worker. Showing dorsal view of petiole and side view of entire body. Pilosity omitted.

midpoint of the anterior genal border. Clypeus bearing an indistinct median carina; its anterior border feebly and evenly convex when viewed in full face. Head when viewed in full face elongate and subrectangular, its sides moderately convex, its greatest width just anterior to the midline, its posterior border very feebly concave, almost straight. Alitrunk and petiole as shown in the accompanying text-figure.

Mandibles smooth and shining; clypeus shallowly punctate and feebly shining to subopaque; remainder of head finely and densely punctate, and completely opaque. Remainder of body feebly punctate to shagreened, and feebly shining to subopaque.

Scattered erect to oblique hairs present on clypeus, occipital region, thorax (but not propodeum), dorsal surface of petiolar node, and entire surfaces of gastric tergites. Standing pilosity completely lacking from appendages, except from funiculi and flexor surfaces of tibiae. Entire body, including appendages, covered by abundant appressed pubescence.

Body uniformly medium brown with reddish undertones; appendages brownish yellow. Some fading may have occurred in this specimen, since in the original description Emery gives the color as "fusca, mandibulis, antennis, pedibus anoque fulvis."

### Ponera tenuis (Emery)

*Cryptopone tenuis* Emery, 1900, Természetr. Füz., 23: 321-322, pl. 8, figs. 21, 22, worker. Original localities: Tamara I., Huon Gulf, and Lemien, near Berlinhafen (= Aitape), N-E. New Guinea. (Syntype examined — Hungarian National Museum.)

*Pseudocryptopone tenuis,* Wheeler, 1933, Amer. Mus. Novitates, no. 672: 13-14.

*Ponera tenuis,* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 373-375, fig. 2, worker, queen, dist., ecology.

### Ponera xenagos Wilson

*Ponera xenagos* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 385-386, worker. Type locality: Tumnang, 1500 m., Huon Pen., N-E. New Guinea.

### Ponera zwaluwenburgi (Wheeler)

*Pseudocryptopone zwaluwenburgi* Wheeler, 1933, Amer. Mus. Novitates, no. 672: 14-16, fig. 5, worker. Type locality: Oahu I., Hawaii.

*Ponera zwaluwenburgi,* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 375-376, worker.

As in the case of the related species *swezeyi,* there is an excellent chance that *zwaluwenburgi* was introduced into the Hawaiian Islands by man, and that it originated somewhere in Melanesia or the East Indies, the present headquarters of the remainder of the *tenuis*-group species.

## The Species of the Fiji Islands

The five known endemic species, all originally described by Mann in his 1921 monograph of the Fijian ant fauna,[1] bear close resemblance to western Melanesian species. If my present interpretation is correct, the Fiji Islands have been populated by three species stocks that are currently among the most widespread in western Melanesia: *biroi* Emery (New Guinea to Solomon Islands), *pruinosa* Emery (Philippines to New Hebrides), and *selenophora* Emery (New Guinea to New Hebrides). In the accompanying table are listed the Fijian species with their presumptive western Melanesian cognates.

Relationships of Fijian *Ponera*

| ENDEMIC FIJIAN SPECIES | CLOSEST RELATED SPECIES IN WESTERN MELANESIA |
|---|---|
| *colaensis* Mann | *selenophora* Emery |
| *eutrepta* Wilson (nom. nov. pro *rugosa* Mann) | *biroi* Emery |
| *monticola* Mann | *pruinosa* Emery |
| *turaga* Mann | *biroi* Emery |
| *vitiensis* Mann | *pruinosa* Emery |

### *Key to the species, based on the worker caste*[2]

1. Petiolar node with distinctly marginate sides. Showing in addition the following combination of sculptural characters: head densely punctate and completely opaque, the alitruncal dorsum sparsely and evenly punctate and mostly shining ..... *colaensis* Mann
   Petiolar node not marginate, its sides broadly and evenly rounded; not showing all of the above sculptural characters ..... 2
2. Head coarsely and densely punctate and completely opaque ..... 3
   Head smooth to moderately punctate and shining over a large part of its surface ..... 4
3. Larger species, head width of single syntype examined 1.09 mm; body color light reddish brown ..... *turaga* Mann

[1] Mann, W. M., 1921, The ants of the Fiji Islands, Bull. Mus. Comp. Zool. Harv., 64: 401-499. Mann does not mention the presence of *P. gleadowi* Forel, but I have seen a worker of this tramp species collected by him at Nadarivatu (MCZ).

[2] Exclusive of the probably introduced *P. gleadowi* Forel.

Smaller species, head width in several nest series examined not greater than 0.91 mm; body color blackish brown ..... *eutrepta* Wilson

4. Eyes containing only a single ommatidium; larger species, head width not less than 0.73 mm; body color light brownish yellow ..... *vitiensis* Mann

Eyes containing 3-4 ommatidia; smaller species, head width not more than 0.63 mm; body color blackish brown ..... *monticola* Mann

### Ponera eutrepta Wilson, nom. nov.

*Ponera biroi* subsp. *rugosa* Mann, 1921, Bull. Mus. Comp. Zool., 64: 415, worker. Type locality: Nadarivatu, Viti Levu, Fiji Islands. *Nec Ponera rugosa* Le Guillou, 1841. (Syntypes examined — MCZ.)

This form seems sufficiently distinct from *biroi* Emery to deserve recognition as a full species. It differs from *biroi* primarily in its larger size, head width varying 0.77-0.91 mm as opposed to 0.64-0.69 mm in *biroi* in the moderate sample examined.[1] Of special interest is the extraordinary variability shown by *eutrepta* in several characters that are only weakly variable in the western Melanesian members of the *biroi* group, namely in total size, in scape index (ranging from 82 to 93 in only four nest series), and in petiole form. Additional collections of *eutrepta* were recently made by the author at Nadala, near the type locality of Nadarivatu, all from rotting logs on the floor of disturbed rain forest (Wilson, nos. 14, 28, 31).

## The Species of New Caledonia

### Ponera caledonica Wilson

*Ponera caledonica* Wilson, 1957, Bull. Mus. Comp. Zool., 116: 361-364, fig. 2, worker, queen. Type locality: Ciu, near Mt. Canala, 300 m., New Caledonia.

This species is a member of the *Ponera tenuis* group and is most closely related to *P. exedra* Wilson of southeastern Australia.

[1] A tendency toward larger size is also exhibited by the Fijian species *turaga* and *vitiensis*, *turaga* reaching the exceptional size for *Ponera* of HW 1.09 mm. It is possible that these species and *eutrepta* tend to replace, ecologically, some of the larger ponerines missing from the Fijian fauna, e.g. *Brachyponera*, *Mesoponera*, and *Trachymesopus*.

### Ponera elliptica Forel, n. status

*Ponera truncata* var. *elliptica* Forel, 1900, Ann. Soc. Ent. Belg., 44: 62, worker, queen. Type locality: none cited, probably in Australia. (Syntype examined — Forel Coll.)

*Ponera truncata* subsp. *elliptica*, Emery, 1914, Nova Caledonia, 1: 397.

*Ponera trigona* subsp. *convexiuscula*, Emery, *ibid.*, p. 398. *?Nec P. trigona* subsp. *convexiuscula* Forel, 1900.

*Material examined.* QUEENSLAND: Mt. Spurgeon, 1100-1600 m. (P. J. Darlington); Malanda (W. L. Brown); Kondalilla National Park, Blackall Range (Brown); Tamborine Mt. (Brown). NEW CALEDONIA: Chapeau Gendarme (Wilson, nos. 65-C, 68, 74, 78, 80, 96): Mt. Mou, 180 m. to summit ridge at 1200 m. (Wilson, nos. 106, 113, 138, 139); Ciu, 300 m (Wilson, nos. 242, 243, 267, 292, 310).

*Taxonomic notes. P. elliptica* is treated here provisionally as a separate species in the absence of definitive information concerning the identity of Frederick Smith's original *Ponera truncata*. Workers from New Caledonia are smaller and more variable in size than those from Queensland. In addition their petiolar nodes in side view are thinner and less symmetrical, showing a very slight anterior curvature absent in Queensland series. *P. elliptica* is very close to *P. pruinosa* Emery and *P. sabronae* Donisthorpe of western Melanesia, being separable only by subtle characters in size, sculpturing, and alitrunk and petiole form.

The New Caledonian population of *elliptica* is very plastic, showing variation in total size, eye size, body form, and sculpturing paralleling that already described for *pruinosa*. It is probable that the specimens referred to by Emery (1914) as *trigona* subsp. *convexiuscula* are nothing more than small *elliptica*, which in fact tend to resemble *convexiuscula* superficially.

*Ecological notes.* Like its Papuan equivalent *P. pruinosa*, *P. elliptica* is an exceptionally abundant and adaptable ant within its range. It was found to be among the more common ant species in most of the localities in southern and eastern New Caledonia visited by the author in 1954-55, extending from dry, semideciduous lowland forest at Chapeau Gendarme to the cool, wet cloud forest on the summit ridge of Mt. Mou. As in *pruinosa*, colonies are generally small. At Chapeau Gendarme they were found nesting exclusively in large rotting logs, while in the moister

forests of Mt. Mou and Ciu they occurred mostly in the soil beneath rocks. On several occasions, at Chapeau Gendarme and Ciu, solitary workers were found foraging during the day on the forest floor.

PONERA GLEADOWI Forel
(See p. 328)

PONERA PERKINSI Forel
(See p. 334)

BRACHYPONERA Emery, n. status

*Euponera* (*Brachyponera*) Emery, 1901, Ann. Soc. Ent. Belg., 45: 43. Generitype: *Ponera sennaarensis* Mayr.

The four subgenera of *Euponera*, viz. *Euponera sensu stricto*, *Brachyponera*, *Mesoponera*, and *Trachymesopus*, seem sufficiently well marked and segregated from each other to deserve provisional generic status. There is even some evidence to suggest that they may be more closely related to other ponerine genera than to each other, as shown for instance in the close link between *Trachymesopus* and *Cryptopone* to be described in a later section.

*Brachyponera* appears to be a fairly recent invader from the Indo-Malayan Region. It is represented in Melanesia by two poorly differentiated species, only one of which (*croceicornis*) ranges as far east as the Solomon Islands.

*Key to the species, based on the worker caste*[1]

1. Sides of the pronotum finely and obliquely striate (Moluccas) ..... *atrata* Karawajew
   Sides of the pronotum finely punctate ..... 2
2. Upper quarter of metapleuron coarsely and transversely striate (character applicable to Papuan samples only); body color dark reddish brown (Neth. New Guinea) ..... *arcuata* Karawajew
   Upper quarter of metapleuron smooth; body color deep blackish brown (New Guinea to Solomon Islands and Queensland) ..... *croceicornis* Emery

[1] Not including *Euponera* (*Brachyponera*) *niger* Donisthorpe, which has recently been shown to be a synonym of *Leptogenys breviceps* Viehmeyer; see Wilson, 1958, Bull. Mus. Comp. Zool. 118: 116.

### Brachyponera arcuata Karawajew, n. status

*Euponera* (*Brachyponera*) *luteipes* var. *arcuata* Karawajew, 1925, Konowia, 4: 125, figs. 3-C, 4, worker, queen, male. Type locality: Tjibodas, Java. Santschi, 1928, Tijdschr. Ent., 71: 124; types restricted to worker and queen, male separated and described as *Leptogenys karawaiewi* Santschi.

I have applied this name provisionally to a single series from Doormanpad, Netherlands New Guinea, collected by W. C. van Heurn (MCZ). This series appears to be conspecific with various Indo-Malayan collections that have been determined as *arcuata* by B. Finzi, W. L. Brown, and others, and seem to fit Karawajew's description well enough. Another Karawajew variety, *B. luteipes* var. *continentalis,* is a possible junior synonym.

In addition to the sculptural and color characters given in the key, the following differences between *arcuata* and *croceicornis* (with *luteipes*) have been noted. (1) In *arcuata* the propodeum is less compressed laterally and its dorsal face is more concex. (2) *Arcuata* is slightly larger in size: the pronotal width of five workers from Doormanpad ranges 0.64-0.67 mm, while that of numerous *croceicornis* workers from New Guinea never measured more than 0.62 mm.

### Brachyponera atrata Karawajew

*Euponera* (*Brachyponera*) *atrata* Karawajew, 1925, Konowia, 4: 126-127, worker. Original localities: Amboina and Boeton. Karawajew, 1926, Treubia, 8:418, queen. Known only from Karawajew's Moluccan type series.

### Brachyponera croceicornis Emery, n. status

*Euponera* (*Brachyponera*) *luteipes* var. *croceicornis* Emery, 1900, Természetr. Füz., 23: 315, worker, queen. Type locality: German New Guinea (L. Biró). (Syntype examined — Emery Coll.)

*Euponera* (*Brachyponera*) *luteipes* subsp. *inops* Forel, 1910, Rev. Suisse Zool., 18: 17, worker. Type locality: Kuranda, Queensland. (Syntype examined — Emery Coll.) NEW SYNONYMY.

*Euponera* (*Brachyponera*) *luteipes,* Karawajew, 1925, Konowia, 4: 124, fig. 3b, worker, *nec B. luteipes* Mayr.

*Ponera bicolor* Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)1: 492, worker. Type locality: Maffin Bay, Neth. New Guinea. (Holotype examined — CAS.) *Nec Ponera bicolor* Guérin, 1845. NEW SYNONYMY.

*Material examined.* NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N-E. NEW GUINEA: Nadzab (Wilson, nos. 1092, 1111); Bubia (Wilson, nos. 676, 683, 1072); lower Busu River (Wilson, nos. 924, 978, 1003, 1024, 1030, 1063); Finsch Harbor (N. G. L. Wagner); Nganduo, 1000 m. (Wilson, no. 733); Nganduo-Yunzain, 1300-1500 m. (Wilson); Joangeng, 1500 m. (Wilson, no. 746); Zingzingu, 1000 m. (Wilson, no. 770); Tumnang, 1500 m. (Wilson, no. 798). PAPUA: Kini-Kini Hill, Port Moresby, 250 m. (Wilson, no. 524); Karema, Brown R. (Wilson, nos. 538, 579); Bisianumu, 500 m. (Wilson, no. 617). SOLOMON ISLANDS: Fulakora, Santa Isabel (W. M. Mann). I have also examined material from northern Queensland.

*Taxonomic notes. B. croceicornis* has been raised to species level provisionally, subject to a more thorough analysis of the related Indo-Malayan forms. The relation of *croceicornis* to *luteipes* is in particular need of further examination, and any such study must start with a re-examination of Mayr's types of *luteipes*, which originated from the Nicobar Islands. At present it is safe to say only that the widespread Indo-Malayan form to which the name *luteipes* has been conventionally applied by past authors differs from *croceicornis* in having the propodeum less compressed laterally and in minor, possibly overlapping characters in sculpturing and pilosity.

On New Guinea, *croceicornis* shows considerable non-geographic variation in the outline of the propodeum, the dorsal border of which when seen in side view is usually feebly concave, but occasionally straight and in one series examined feebly convex. There is also much variation in the abundance of body pilosity, with a marked secondary effect on the degree of cuticular shininess in reflected light.

*Ecological notes.* This species is one of the most abundant and wide-ranging ants in New Guinea, occurring from sea level to at least 1500 meters on the Huon Peninsula alone, and in a wide variety of major habitats, from dry semi-deciduous woods (near Port Moresby) to primary lowland rain forest (Busu River). Colonies nest in small "passalid-stage" logs on the forest floor and usually contain a single dealate queen and less than 100 workers. Workers forage singly on the ground during the day, and are so abundant in this situation that strays can usually

be turned up within an hour in most localities by persistent leaf-litter collecting. At Nadzab a worker was found carrying a small, recently killed spider in its mandibles.

### Mesoponera Emery, n. status

*Euponera* (*Mesoponera*) Emery, 1901, Ann. Soc. Ent. Belg., 45: 43. Generitype: *Ponera caffraria* Fr. Smith.

This genus shows a zoogeographic pattern almost identical with that already described for *Brachyponera*. Only two species are known from Melanesia. Both are limited to the western archipelagoes and have primarily Indo-Malayan affinities.

### Mesoponera manni Viehmeyer

*Euponera* (*Mesoponera*) *papuana*, Mann, 1919, Bull. Mus. Comp. Zool., 63: 290-291, fig. 8, worker. *Nec. Euponera papuana* Viehmeyer, 1914. Original localities: Wai-ai, San Cristoval, and Fulakora, Santa Isabel, Solomon Islands.

*Euponera* (*Mesoponera*) *manni* Viehmeyer, 1924, Ent. Mitt., 13: 228, nom. pro *Euponera* (*Mesoponera*) *papuana*, Mann, 1919. (Syntype examined — MCZ.)

*Euponera* (*Mesoponera*) *robiginosa* Donisthorpe, 1941, Ann. Mag. Nat. Hist., (11)7: 131, worker. Type locality: Sabron, Cyclops Mts., Neth. New Guinea. NEW SYNONYMY (provisional).

*Material examined.* N-E. NEW GUINEA: Bandong, Bunbok Valley, 1300 m. (Wilson, no. 1124). SOLOMON ISLANDS: Fulakora, Santa Isabel (syntype).

*Taxonomic notes.* This form is closely related to, and possibly conspecific with, the Indo-Malayan species *M. rubra* (Fr. Smith). More material from over the ranges of both species is needed before their relationship can be exactly determined. *M. manni* differs from the sympatric *M. papuana* as follows. (1) The petiolar node of *manni* resembles that of *melanaria* and *australis* as opposed to that of *papuana* (see also under *papuana*). (2) *Manni* differs from *papuana*, and also *melanaria* and *australis*, by its notably smaller eye size (eye length 0.13 mm as opposed to 0.15 mm). *M. rubra*, however, has an almost exactly intermediate eye size. (3) The body color of *manni* is light to medium

reddish brown, that of *papuana* and *melanaria* always blackish brown. *Australis* is usually blackish brown but occasional specimens are as light as *manni*.

*Ecological notes.* Mann collected the type workers from a colony nesting in a rotting log in lowland rain forest. My Bandong, New Guinea specimens were found under a rock in a partial clearing in midmountain rain forest.

### Mesoponera papuana Viehmeyer

*Euponera* (*Mesoponera*) *papuana* Viehmeyer, 1914, Zool. Jahrb. Syst., 37: 608-609, worker. Type locality: Wareo, N-E. New Guinea.

*Euponera* (*Mesoponera*) *melanaria* subsp. *papuana* Viehmeyer, 1924, Ent. Mitt., 13: 228.

*Euponera* (*Mesoponera*) *pulchella* Donisthorpe, 1941, Ann. Mag. Nat. Hist., (11)7: 133, worker, queen. Type locality: Mt. Lina, 1100 m., Cyclops Mts., Neth. New Guinea. NEW SYNONYMY (provisional).

*Euponera* (*Mesoponera*) *viehmeyeri* Donisthorpe, 1948, Ann. Mag. Nat. Hist., (12)1: 132, worker. Type locality: Maffin Bay, Neth. New Guinea. NEW SYNONYMY (provisional).

*Material examined.* NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N-E. NEW GUINEA: lower Busu River (Wilson, acc. nos. 892, 994).

*Taxonomic notes.* The taxonomy of *M. papuana* and its Indo-Australian relatives, comprising the *melanaria* group, has been notoriously confused in the past, due to reliance placed by older workers on inadequate series and their consistent employment of morphological characters that appear now to be of little or no diagnostic value. In the case of Donisthorpe's species of *Mesoponera*, their status can be settled finally only by consulting type material.

During the present study I have had the opportunity to examine an unusually large number of series belonging to the *melanaria* group, including *melanaria* Emery mostly from Ceylon, *rubra* (Fr. Smith) from Java, *papuana* Viehmeyer from New Guinea, and *australis* Forel from Queensland. The sample is still quite small, and the taxonomy of the group cannot yet be considered stable, but it is at least possible now to indicate some characters of probable diagnostic value.

It should first be noted that within the *melanaria* group, *melanaria* and *australis* are more closely related to each other than to any other species. Apparently the only discontinuous character that can be used to separate them, and therefore serve as an excuse to recognize them as distinct species, is the following. In *australis* the pronotum always bears two or more erect hairs set in distinct pits; usually there are two such hairs, symmetrically situated. In *melanaria,* the pronotum is invariably bare of pits and standing hairs.

*Papuana,* although occupying a geographically intermediate range between those of the closely related *melanaria* and *australis,* has morphological characters that set it off from both of these forms:

(1) In *papuana,* the median portion of the dorsal petiolar border appears slightly indented when the petiole is viewed frontally. Seen from directly above, the dorsal border appears indented in an anterior direction at its midpoint. In *melanaria* and *australis,* the dorsal petiolar border forms an even, continuously convex curve when the petiole is viewed frontally; when viewed from directly above, the border does not appear indented medially.

(2) In *papuana* there are invariably one or two coarse, standing hairs present on the first gastric tergite, and usually three or more on the second gastric tergite. In *melanaria* and *australis* the first tergite is always bare, while the second is either bare or has at most one or two standing hairs.

A special note is required here concerning the provisional synonymy of Donisthorpe's two forms *viehmeyeri* and *pulchella.* A worker from the type locality of *viehmeyeri* compared with a syntype of *viehmeyeri* by Dr. E. S. Ross agrees with my conception of *papuana.* The original description of *pulchella* does not depart from *papuana* in any detail. Further, Donisthorpe gives no indication in the descriptions of either form that he was aware of Viehmeyer's prior name, and he takes no account of the better known, closely related *australis.*

*Ecological note.* A colony of *papuana* collected entire at the Busu River consisted of a single dealate queen, 8-10 workers, and a small quantity of brood in all stages of development. The ants were nesting in a small section of rotting tree branch buried

in the soil beneath a larger, more recently fallen rotting log. In another section of the Busu Forest workers were observed foraging during the day in thin leaf litter accumulated between the buttresses of a large tree.

### Trachymesopus Emery, n. status

*Euponera* (*Trachymesopus*) Emery, 1911, Genera Insectorum, 118: 84. Generitype: *Formica stigma* Fabricius.

As Wheeler showed in his 1933 revision of *Cryptopone*,[1] this genus is more closely related to *Trachymesopus* than to *Ponera*, the genus with which it had been associated and often confused in the past. The connection is so close, in fact, as to render the generic integrity of *Trachymesopus* debatable. In the present study I have had the opportunity of examining a large percentage of the described species of *Cryptopone* and *Trachymesopus*, including the type species of both genera. Within the limits of this sample I have been able to separate the two genera by means of the following worker characters:

(1) In *Trachymesopus* secondary spurs are well developed on the middle and hind tibiae, being at least one-third as long as the primary, pectinate spurs. In *Cryptopone* secondary spurs are completely lacking, or at least are not visible in magnifications up to 90×.

(2) The mandibles of *Trachymesopus* are broader, and the masticatory borders tend to be more nearly parallel (opposable) with one another.

(3) Compound eyes are nearly always present in *Trachymesopus*, even though greatly reduced in size in some species; the apparent eyeless exception is the Palaearctic species *T. ochracea* (Mayr). In contrast, all of the species of *Cryptopone* are completely eyeless.

Due to our incomplete knowledge of the smaller species, no attempt will be made here to key the Melanesian *Trachymesopus*. *T. sheldoni* is known solely from the holotype worker, while *T. darwini* is apparently represented in collections only by winged queens taken at lights.

[1] Wheeler, W. M. 1933. Three obscure genera of ponerine ants. Amer. Mus. Novitates, no. 672: 1-23.

### Trachymesopus darwini (Forel)

*Belonopelta Darwinii* Forel, 1893, Ann. Soc. Ent. Belg., 37: 460-461, queen. Type locality: Darwin, N. T., Australia.

*Material examined.* NETH. NEW GUINEA: Maffin Bay, winged queens, July 8, 1944 (E. S. Ross). N-E. NEW GUINEA: lower Busu River, winged queens, May 16, 1955 (Wilson, no. 1112). NEW HEBRIDES: Ratard Plantation, Luganville, Espiritu Santo, winged queen, January 7-13, 1955 (Wilson).

*Taxonomic note.* The Melanesian series cited above, consisting of winged queens taken at light, all appear to be conspecific, but assignment to Forel's Australian-based *darwini* is quite tentative. Both *darwini* and its better known Indo-Malayan variety *indica* Forel appear to be known only from the queen caste, and there is little hope of correctly assigning these forms with respect to the remainder of *Trachymesopus* until additional material, including definitely associated workers, is made available.

### Trachymesopus crassicornis (Emery)

*Belonopelta crassicornis* Emery, 1897, Ann. Mus. Stor. Nat. Genova, 18: 553-554, queen. Type locality: Moroka, 1300 m., Papua. (Holotype examined — Emery Coll.)

*Euponera* (*Trachymesopus*) *crassicornis*, Emery, 1911, Genera Insectorum, 118: 86.

*Material examined.* N-E. NEW GUINEA: Joangeng, 1500 m., Huon Pen. (Wilson, no. 747). PAPUA: (holotype). SOLOMON ISLANDS: Boku, Bougainville, dealate queen, June 4, 1956 (E. J. Ford, Jr.).

*Taxonomic notes.* The holotype queen, kindly loaned to the author by Dott. Delfa Guiglia, is labeled as follows: "Belonopelta crassicornis — typus — Moroka, 1300 m., N. Guinea S. E. — Loria, VII-IX, '93." This is in contradiction with the type locality cited in the original description, which is Kapa-Kapa. Moroka has been provisionally accepted here as the correct type locality.

The queen collected by the author at Joangeng appears to differ from the holotype only in its somewhat smaller size; its head width is 0.98 mm as opposed to 1.03 mm in the holotype. The queen from Boku, Bougainville, is intermediate in size (head width 1.00 mm) but differs from the New Guinea specimens

in its slightly narrower petiolar node and concave anterior node face. This individual may be referable to the related *T. sheldoni*, at present known only from a single worker from San Cristoval (*q. v.*).

*Ecological note.* At Joangeng a small colony of *crassicornis*, consisting of a single dealate queen and an undetermined number of workers and males, was found during April 7-8, 1955, in a "passalid-stage" log in second-growth midmountain rain forest.

### Trachymesopus rotundiceps Emery

*Euponera* (*Trachymesopus*) *rotundiceps* Emery, 1914, Nova Caledonia, 1: 397, queen. Type locality: Mt. Canala, 700 m., New Caledonia.

*Material examined.* NEW CALEDONIA: Mt. Mou (Wilson, no. 105). I have also seen material of this species collected in Queensland, at Malanda (W. L. Brown), Lake Barrine (P. J. Darlington), and in the Paluma Range, near Townsville (E. O. Wilson).

*Taxonomic note.* Workers from Malanda, Queensland, differ from New Caledonian *rotundiceps* in their smaller size, proportionately smaller eyes, and less compressed propodeum, but overall seem close enough to be conspecific.

*Ecological note.* At Mt. Mou stray workers of this species were found in cavities in moss-covered bark lying on top of a large, moist, rotting log.

### Trachymesopus sheldoni Mann

*Euponera* (*Trachymesopus*) *sheldoni* Mann, 1919, Bull. Mus. Comp. Zool., 63: 292, worker. Type locality: Wainoni Bay, San Cristoval, Solomon Islands.

At my request Dr. M. R. Smith has compared the holotype of *sheldoni*, on deposit in the U. S. National Museum, with a verified *crassicornis* worker from Joangeng, New Guinea. He is of the opinion that *sheldoni* is specifically distinct from *crassicornis*, differing principally in the seven characters listed below (*in litt.*).

(1) *Crassicornis* is larger and stouter.

(2) The head of *sheldoni* is proportionately longer and with more nearly parallel sides.

(3) The antennal scape of *sheldoni* is not so slender at the base nor so abruptly enlarged at the apex as in *crassicornis*.

(4) *Crassicornis* has the base of the propodeum more compressed.

(5) The petiolar node of *crassicornis* is broader dorsally in proportion to its (antero-posterior) length. *Sheldoni* has what appears to be an impressed area extending from the posterior surface of the node dorsally to the dorsal border.

(6) The cephalic and pronotal sculpturing of *crassicornis* is much coarser.

(7) The body color of *sheldoni* is yellowish ("callow-like"), as opposed to medium brown in *crassicornis*.

### Trachymesopus stigma (Fabricius)

*Formica stigma* Fabricius, 1804, Syst. Piez., p. 400, queen. Type locality: "America meridionali."

*Ponera quadridentata* Fr. Smith, 1859, Jour. Linn. Soc. Zool., 3: 143, queen. Type locality: Aru. NEW SYNONYMY.

*Pachycondyla* (*Pseudoponera*) *stigma* var. *quadridentata*, Emery, 1900, Természetr. Füz., 23: 314-315, worker, queen.

*Euponera* (*Trachymesopus*) *stigma* var. *quadridentata*, Emery, 1911, Genera Insectorum, 118: 85. Karawajew, 1925, Konowia, 4: 127, ecology.

*Euponera* (*Trachymesopus*) *nixoni* Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)10: 441, queen. Type locality: Camp Nok, 800 m., Waigeo. *Ibid.*, (11)14: 299, worker. (Holotype examined — see below.) NEW SYNONYMY.

*Euponera* (*Trachymesopus*) *brunneus* Donisthorpe, 1947, Ann. Mag. Nat. Hist., (11)14: 300-301, worker, queen. Type locality: Maffin Bay, Neth. New Guinea. (Paratypes examined — CAS.) NEW SYNONYMY.

*Euponera* (*Trachymesopus*) *sexdentatus* Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)1: 746, worker. Type locality: Maffin Bay, Neth. New Guinea. (Holotype examined — CAS.) NEW SYNONYMY.

*Material examined.* NETH. NEW GUINEA: Maffin Bay (numerous series; E. S. Ross). N-E. NEW GUINEA: Nadzab (Wilson, no. 1101); lower Busu River (Wilson, no. 1013). PAPUA: Karema, Brown R. (Wilson, no. 566); Bisianumu, 500 m. (Wilson, no. 643). SOLOMON ISLANDS: Tulagi, Florida (W. M. Mann); Ugi (Mann); Fulakora, Santa Isabel (Mann); Rubiana Lagoon, New Georgia (Mann); Pamua and

Wai-ai, San Cristoval (Mann). FIJI ISLANDS: Lasema, Vanua Levu (Mann). I have also seen material of this species from China (vicinity of Amoy), Philippines, and Samoa.

*Taxonomic notes.* I have compared series of all three castes of Pacific *stigma* (= var. *quadridentata*) against those from the Neotropical Region and am unable to find any satisfactory separatory characters. *Stigma*, as now broadly conceived to include *quadridentata*, occupies a vast range. In the New World it occurs from southern Florida through the Antilles and Central America to as far south as the upper Amazon Valley. In the Old World it occurs from southern China to Samoa. In both hemispheres it has been collected from the interior of relatively undisturbed native forests, where it lives in apparent compatibility with local endemic ant faunas of the most diverse kinds. The center of origin of *stigma* is unknown, but the New World tropics seem the most likely possibility, since the most closely related species occur there.

Types of *T. brunneus* Donisthorpe and *T. sexdentatus* Donisthorpe examined by me appear identical with Papuan *stigma*. Dr. G. E. J. Nixon has compared the holotype of *T. nixoni* Donisthorpe, on deposit in the British Museum (Natural History), with *stigma* workers from Bisianumu, Papua, and finds them to be nearly or entirely identical (Nixon, *in litt.*).

*Ecological notes.* On New Guinea this species is found in both primary and disturbed rain forests. It appears to nest exclusively under the bark of large "Zoraptera-stage" or "passalid-stage" logs, often in company with *Myopopone castanea* (Fr. Smith).[1] Workers forage singly and may range over as much as eight meters distance through the subcortical spaces of the log. Colonies are apparently often diffuse in structure. At Karema, for instance, an isolated group of about ten workers were found clustered around several larvae; intensive search in the immediate vicinity failed to turn up a queen or additional brood. Colonies may apparently be founded by lone dealate queens. At Bisianumu several such queens were found scattered over a large rotting log, apparently in the act of searching for suitable nesting sites.

[1] Karawajew (1925) found a colony under similar conditions on Wammar, Aru, nesting in "Gängen in einem faulen liegenden Baumstamm, im Urwald."

## Cryptopone Emery

*List of the species of Melanesia and the Moluccas, with new synonymy*

*butteli* Forel
*fusciceps* Emery
=*Cryptopone mayri* var. *fuscior* Mann
=*Cryptopone mayri* var. *minor* Mann
*motschulskyi* Donisthorpe
*testacea* Emery
=*Cryptopone mayri* Mann
=*Cryptopone emeryi* Donisthorpe
=*Ponera anommata* Donisthorpe

At least two of the Melanesian *Cryptopone* (*butteli, testacea*) also occur widely through the Indo-Malayan Region and Micronesia. *C. motschulskyi*, the only species restricted to New Guinea and Waigeo, is the largest member of the genus, falling well within the lower size limit of *Trachymesopus*. In eastern New Guinea at least, it appears to replace *Trachymesopus* ecologically.

*Key to the species, based on the worker caste*

1. Mandibles 5-toothed ..... 2
   Mandibles 6-toothed ..... 3
2. Head length almost exactly equal to head width; when scapes are laid against the head and aligned with the long axis of the head, and when the head is viewed in perfect full face, the tips of the scapes just reach the occipital border ..... *butteli* Forel
   Head length exceeding 1.1 X the head width; when scapes are aligned and viewed as described above, their tips fail to reach the occipital border by about their maximum width ..... *fusciceps* Emery
3. Smaller species, head width never exceeding 0.59 mm and usually much less (single queen available, from Ceylon, is medium yellowish brown and small, the head width across and including eyes 0.64 mm) ..... *testacea* Emery
   Larger species, head width at east 0.64 mm and usually much more (queen dark brown and large, head width at least 0.88 mm) ..... *motschulskyi* Donisthorpe

### Cryptopone butteli Forel

*Cryptopone butteli* Forel, 1913, Zool. Jahrb. Syst., 36: 9-10, fig. C, worker. Original localities: Beras Tagi, 1450 m., Sumatra, and Buitenzorg, Java. Wheeler, 1933, Amer. Mus. Novitates, no. 672: 9-11, fig. 3, queen, male.

*Material examined.* N-E. NEW GUINEA: lower Busu River (Wilson, nos. 962, 984, 998, 999, 1058); Joangeng, 1500 m. (Wilson, no. 746)); Zingzingu, 1000 m. (Wilson, no. 768); Ebabaang, 1300-1400 m. (Wilson, no. 836). NEW BRITAIN: St. Paul's, 350 m., Bainings Mts., Gazelle Pen (J. L. Gressitt).

*Ecological notes.* On the Huon Peninsula *butteli* occurs in rain forest through a wide range of elevation. Colonies are relatively small, containing probably less than 30 adult members, and are found nesting both in rotting logs and in the soil beneath rocks. This was one of the few ant species found nesting under rocks in primary lowland rain forest at the Busu River. Workers were encountered on several occasions foraging singly in humus and (at higher elevations) under moss beds covering the ground. They are very timid and sluggish in their movements. Winged males were taken in a nest at the Busu River on May 10, 1955.

### Cryptopone fusciceps Emery

*Cryptopone fusciceps* Emery, 1900, Természetr. Füz., 23: 321, pl. 8, figs. 19, 20, worker, queen. Type locality: Lemien, near Berlinhafen (= Aitape), N-E. New Guinea. (Syntype examined — Emery Coll.)

*Cryptopone mayri* var. *fuscior* Mann, 1919, Bull. Mus. Comp. Zool., 63: 294, worker. Type locality: Fulakora, Santa Isabel, Solomon Islands. (Syntype examined — MCZ.) NEW SYNONYMY.

*Cryptopone mayri* var. *minor* Mann, 1919, *ibid.*, p. 294, in key. Objective synonym of *C. mayri* var. *fuscior* Mann. NEW SYNONYMY.

*Cryptopone fuscior*, Wheeler, 1933, Amer. Mus. Novitates, no. 672: 8, fig. 2, worker.

*Material examined.* N-E. NEW GUINEA: Lemien (syntype); Mt. Hansemann, near Madang (L. Biró); lower Busu River (Wilson, nos. 939, 954, 961, 1033); Gemeheng, 1300 m. (Wilson, no. 786); Ebabaang, 1300-1400 m. (Wilson, nos. 824, 828). SOLOMON ISLANDS: Fulakora, Santa Isabel (*fuscior* syntype).

*Taxonomic notes.* The material cited above shows significant variation in size (HW 0.41-0.47 mm), in thickness of the petiolar

node, and in conformation of the anterior node face (feebly concave to plane). Head color varies from distinctly darker than that of the alitrunk to nearly equal to it in shade. Montane series (Mt. Hansemann, Gemeheng, Ebabaang) average slightly larger in size than lowland series.

It should be noted here that all of the *fusciceps* workers examined by the author, including a syntype from the Emery Collection, are completely eyeless, conforming to the rest of the genus and contrary to the statement of Emery in the original description.

*Ecological notes.* All of the author's accessions consisted of workers foraging singly in leaf litter and rotting logs in rain forest.

### Cryptopone motschulskyi Donisthorpe

*Cryptopone motschulskyi* Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)9: 167, queen. Type locality: Camp Nok, 800 m., Waigeo. (Syntype examined by G. E. J. Nixon — BMNH.)

*Material examined.* N-E. NEW GUINEA: lower Busu River (Wilson, acc. nos. 877, 895, 932, 943, 1021, 1046, 1063); Bubia (Wilson, nos. 681, 683, 1063, 1075). PAPUA: Bisianumu, 500 m. (Wilson, nos. 604, 619, 623, 644, 668).

*Ecological notes.* This species is apparently limited to lowland and foothills rain forest where in eastern New Guinea at least it is quite abundant. It nests almost exclusively in rotting logs on the forest floor. Colonies and stray workers have been found in logs from approximately ten centimeters to more than a meter in diameter and in all stages of decomposition from "Zoraptera-stage" to "passalid-stage." On a single occasion individuals were found in preformed cavities in a polypore fungus growing on top of a large rotting log. The workers are exceptionally large for *Cryptopone* and in general appearance and behavior closely resemble *Trachymesopus*. It was evident that at the several localities where *motschulskyi* was encountered, this species had almost entirely replaced *Trachymesopus* in the available nest sites in rotting logs, a habitat where *Trachymesopus* is prominent in many other parts of the world.

### Cryptopone testacea Emery

*Cryptopone testaeca* Emery, 1893, Ann. Soc. Ent. Fr., pp. 240-241, pl. 6, figs. 3, 4, worker. Type locality: Nawalapitya, Ceylon. *Nee ?Amblyopone testacea* Motschulsky, 1863, Bull. Soc. Nat. Moscou, 36: 15, queen. (Syntype examined — Emery Coll.)

*Cryptopone mayri* Mann, 1919, Bull. Mus. Comp. Zool., 63: 293, worker, queen. Type locality: Fulakora, Santa Isabel, Solomon Islands. Wheeler, 1933, Amer. Mus. Novitates, no. 672: 7-8, fig. 1, worker. (Syntype examined — MCZ.) NEW SYNONYMY.

*Cryptopone sarawakana* Wheeler, 1933, *ibid.*, pp. 11-12, fig. 4, worker, male. Type locality: Mt. Poi, Sarawak. (Syntype examined — MCZ.) NEW SYNONYMY.

*Cryptopone emeryi* Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)9: 168, nota, nom. pro *C. testacea* Emery, 1893. Objective synonym of *C. testacea* Emery. NEW SYNONYMY.

*Ponera anommata* Donisthorpe, 1947, Ann. Mag. Nat. Hist., (11)14: 301-302, worker, male. Type locality: Maffin Bay, Neth. New Guinea. (Holotype examined — CAS.) NEW SYNONYMY.

*Material examined.* NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N-E. NEW GUINEA: lower Busu River (Wilson, no. 977). SOLOMON ISLANDS: Pawa, Ugi; Pamua, San Cristoval (*mayri* syntypes). This species is widely distributed from Ceylon to the Solomon Islands and Micronesia.

*Taxonomic notes.* As previously pointed out by Wheeler (1933) and Donisthorpe (1943), the dimensions given by Motschulsky for the *Amblyopone testacea* type queen, namely, total length 2 lines (= 4.2 mm), head width 0.4 lines (= 0.85 mm, roughly), would seem too large for this specimen to be conspecific with the worker series identified as *testacea* by Emery in 1893. I have since collected Emery's *testacea* in Ceylon,[1] and can definitely confirm this size disparity. The single queen in this series yields the following measurements: total length measured in a direct line from the tip of the mandibles to the tip of the gaster, 2.8 mm; total length derived as the sum of the individual lengths of the head, alitrunk, pedicel, and gaster, 3.7 mm; head width across and including eyes, 0.65 mm. There is an excellent possibility that Motschulsky's queen is really a

[1] Gilimale, 16-20 km. northeast of Ratnapura, Ceylon; July 18-21, 1955; workers, winged queen, male (Wilson, no. 1309).

*Trachymesopus,* such as *T. indica* Emery or *T. rufotestacea* (Donisthorpe).[1] But in any case, it is probably not a *Cryptopone* and is almost certainly not the species described by Emery as *Cryptopone testacea.* Accordingly, it is proposed that *Amblyopone testacea* Motschulsky be left for the time being as a *nomen dubium,* and Emery's 1893 description be accepted as the original one for *Cryptopone testacea.*

Syntypes of *mayri* Mann and *sarawakana* Wheeler have been compared directly with a syntype of *testacea* and appear to be conspecific. It should be noted that minor differences between these series in head and petiolar node shape have been exaggrated in Wheeler's figures, and that Wheeler miscounted the number of mandibular teeth in the *mayri* types.

*Ecological note.* At the Busu River, New Guinea, and Gilimale, Ceylon, small colonies of *testacea* were found nesting in large, rotting, "passalid-stage" logs on the floor of lowland rain forests.

## Bothroponera Mayr

*Bothroponera* Mayr, 1862, Verh. Zool.-bot. Ges. Wien, 12: 717. Generitype: *Ponera pumicosa* Roger.

*Pseudoneoponera* Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)10: 439. Generitype: *Pseudoneoponera verecundae* Donisthorpe. (Monobasic.) NEW SYNONYMY.

During a recent visit to the British Museum (Natural History) I had the opportunity of examining the unique male type of *Pseudoneoponera verecundae* Donisthorpe in some detail. This specimen is almost certainly a *Bothroponera,* resembling definitely associated males of other species of that genus in most major features of external morphology. The character emphasized by Donisthorpe in erecting his new genus (and new section, Exeuponerinae),[2] the retractibility of the male genitalia, is shared by at least some of the species of *Bothroponera.* The type of *verecundae* is extremely close to two isolated Bornean males tentatively determined as *Bothroponera tridentata* (Fr. Smith)

[1] *Cryptopone rufotestaccus* Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)10: 197-199, queen. Type locality: Tenmalai, Travancore, India. *Ad Trachymesopus.* NEW COMBINATION. A syntype queen in the MCZ is unquestionably a *Trachymesopus.* The relationship of *rufotestaceus* to *indica* and other Indo-Malayan forms has not been investigated.

[2] Ponerini Forel = Exeuponerinae Donisthorpe. NEW SYNONYMY.

in the Museum of Comparative Zoology collection, but of course its relationship to this species and to the two worker-based Papuan species of *Bothroponera* (*incisa* and *obesa*) cannot be settled until worker-male associations are made.

### Bothroponera incisa Emery

*Pachycondyla* (*Bothroponera*) *incisa* Emery, 1910, Nova Guinea, 5 (zool.): 533, fig. 1, worker. Type locality: Manokwari, Neth. New Guinea.

### Bothroponera obesa Emery

*Ponera* (*Bothroponera*) *obesa* Emery, 1897, Ann. Mus. Stor. Nat. Genova, 38: 551, worker. Type locality: Ighibirei, New Guinea.

### Bothroponera solitaria (Fr. Smith)

*Ponera solitaria* Fr. Smith, 1860, Jour. Linn. Soc. Zool., 5: 103, male. Type locality: Batjan. *Nec Ponera solitaria* Fr. Smith, 1873.

*Pachycondyla* (*Bothroponera*) *solitaria*, Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 461.

### Bothroponera verecundae (Donisthorpe), n. comb.

*Pseudoneoponera verecundae* Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)10: 439, male. Type locality: Camp Nok, 800 m., Waigeu.

## Ectomomyrmex Mayr

### *Key to the species, based on the worker caste*[1]

1. Posterior face of the petiolar node completely covered by coarse, straight, evenly spaced longitudinal striae; first and second gastric tergites covered by similar striae; sculpturing of the frontal area of the head consisting of dense longitudinal rugae that give way posteriorly to a section of transverse rugae occupying the central portion of the occipital zone ..... *striatulus* Karawajew

   Posterior face of the petiolar node sculptured otherwise: either the striae are oblique and converge dorsally toward the midline, or transverse, or sparse and irregularly oriented; remainder of body not showing all of the additional sculptural characters described above ..... 2

[1] Exclusive of *vermiculatus* (Emery), known only from Tenimbar.

2. Striation of first gastric tergite concentric-semicircular and always strongly developed ..... 3
   Striation of first gastric tergite straight and longitudinal and often only feebly developed ..... 4
3. Striation of second gastric tergite concentric-semicircular; "center" of concentricity of striae of first gastric tergite located posterior to the midpoint of the dorsal tergital midline ..... *aciculatus* Emery
   Striation of second gastric tergite straight and longitudinal; "center" of concentricity of striae of first gastric tergite located anterior to the midpoint of the dorsal tergital midline ..... *scobinus* Wilson
4. Striae of dorsal surface of first gastric tergite very fine and much obscured by prominent, broad, shallow, contiguous punctures that fill the interspaces ..... 5
   Striae of dorsal surface of first gastric tergite strongly developed and not obscured by the interspace punctures, which are fine and scattered ..... 6
5. Striation of posterior face of petiolar node transverse (Solomon Islands) ..... *aequalis* Mann
   Striation of posterior face of petiolar node oblique and converging dorsally toward the midline (Neth. New Guinea) ..... *simillimus* (Donisthorpe)
6. Striation of posterior surface of petiolar node predominantly transverse; entire second gastric tergital surface covered by striae ..... *acutus* Emery
   Striation of posterior surface of petiolar node predominantly oblique and converging dorsally toward the midline; only the posterior half of the second gastric tergite striate, the remainder smooth ..... *exaratus* Emery

### Ectomomyrmex aciculatus Emery

*Pachycondyla* (*Ectomomyrmex*) *aciculata* Emery, 1902, Természetr. Füz., 25: 157, worker. Original localities: Simbang and Sattelberg, N-E. New Guinea. (Syntype examined — Emery Coll.)

*Material examined.* N-E. NEW GUINEA: lower Busu River (Wilson, nos. 704, 1008, 1036).

*Ecological notes.* Workers of this species were encountered commonly in the Busu Forest, where they were foraging during the day on the forest floor, moving through and under loose leaf litter. Two individuals were found carrying prey, in one case a small, newly-molted millipede and in the other a small ground-dwelling spider.

### Ectomomyrmex acutus Emery

*Pachycondyla* (*Ectomomyrmex*) *acuta* Emery, 1900, Természetr. Füz., 23: 314, worker. Type locality: Tamara I., Huon Gulf, N-E. New Guinea.

*Ponera* (*Ectomomyrmex*) *Dahlii* Forel, 1901, Mitt. Zool. Mus. Berlin, 2(1, b): 9, worker. Type locality: Kabakaul, New Britain. NEW SYNONYMY (provisional).

*Ectomomyrmex exarata*, Mann, 1919, Bull. Mus. Comp. Zool., 63: 288-289, worker. *Nec exarata* Emery, 1902.

*Material examined.* SOLOMON ISLANDS: Fulakora, Santa Isabel (W. M. Mann).

### Ectomomyrmex aequalis Mann, n. status

*Ectomomyrmex exarata* subsp. *aequalis* Mann, 1919, Bull. Mus. Comp. Zool., 63: 289, Fig. 7, worker. Type locality: Auki, Malaita, Solomon Islands (by present selection). (Syntypes examined — MCZ.)

*Material examined.* SOLOMON ISLANDS: Auki, Malaita: Tulagi, Florida (syntypes).

### Ectomomyrmex exaratus Emery

*Pachycondyla* (*Ectomomyrmex*) *exarata* Emery, 1902, Természetr. Füz., 25: 156-157, worker. Original localities: Simbang, Sattelberg, and Mt. Oertzen, N-E. New Guinea. (Syntype examined — Emery Coll.)

*Material examined.* N-E. NEW GUINEA: lower Busu River (Wilson, no. 1052); Bubia (Wilson, no. 681).

*Taxonomic note.* The Busu River and Bubia specimens differ from a worker syntype in the Emery Collection only in their somewhat smaller size.

*Ecological note.* Both the Busu River and Bubia collections consisted of workers found foraging during the day on the rain forest floor.

### Ectomomyrmex insulanus (Mayr)

*Ponera insulana* Mayr, 1876, Jour. Mus. Godeffroy, 12: 87, worker. Type locality: Samoa.

*Pachycondyla* (*Ectomomyrmex*) *insulana*, Emery, 1901, Ann. Soc. Ent. Belg., 45: 46.

Mention is made here of this Samoan species because of its unusual extralimital distribution with respect to the rest of the

genus and the possibility that it or a related species may eventually be discovered within Melanesia. Judging from Mayr's description, *insulanus* should be distinguishable from the known Melanesian species by its very light, non-striate gastric sculpturing: "abdomen haud dense punctatum et modice nitens, segmento primo fortius punctato et minus nitente."

### Ectomomyrmex scobinus Wilson, nom. nov.

*Bothroponera striata* Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)1: 489, worker. Type locality: Maffin Bay, Neth. New Guinea. (Syntype examined — CAS.) *Nec Pachycondyla* (*Ectomomyrmex*) *striata* Karawajew, 1927.

Known from type material only.

### Ectomomyrmex simillimus (Donisthorpe), n. comb.

*Bothroponera simillima* Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)1: 490, worker, queen. Type locality: Maffin Bay, Neth. New Guinea. (Syntype examined — CAS.)

*Material examined.* NETH. NEW GUINEA: Maffin Bay (syntype). N-E. NEW GUINEA: lower Busu River (Wilson, no. 878).

*Ecological note.* My accession no. 878 consists of a stray dealate queen collected from the floor of primary lowland rain forest.

### Ectomomyrmex striatulus Karawajew

*Pachycondyla* (*Ectomomyrmex*) *striata* Karawajew, 1927, Mém. Acad. Sci. Ukraine (Sci. Phys. Math.), 7: 5, worker. Type locality; Amboina. *Nec Pachycondyla striata* Fr. Smith, 1858.

*Pachycondyla* (*Ectomomyrmex*) *striatula* Karawajew, 1935, Treubia, 15: 70, nom. pro. *P. striata* Karawajew.

*Material examined.* N-E. NEW GUINEA: Wamuki, 800 m., Huon Pen. (Wilson, nos. 851, 857); Didiman Creek, Lae (Wilson, no. 694). PAPUA: Karema, Brown R. (Wilson, nos. 532, 566).

*Ecological notes.* Three colonies of this species were found, two at Wamuki and one at Karema. All were small, comprising less than 100 workers, and were nesting in small rotting logs on the ground. A single dealate queen was collected with the Karema

colony. As in most or all other species of *Ectomomyrmex,* the workers curl up into a pupa-like position and feign death for a moment when disturbed. Unlike the workers of *Bothroponera,* they do not emit strings of bubbles from the tip of the gaster as a defense response.

### Ectomomyrmex vermiculatus (Emery)

*Pachycondyla* (*Bothroponera*) *vermiculata* Emery, 1897, Ann. Mus. Stor. Nat. Genova, (2)18: 552, nota, queen. Type locality: Tenimbar.

*Pachycondyla* (*Ectomomyrmex*) *vermiculata,* Emery, 1911, Genera Insectorum, 118: 79.

The only truly diagnostic feature given by Emery in the original description is the sculpturing of the first gastric tergite, which is said to consist of longitudinal striae finer than those on the head. Two of the other known Melanesian *Ectomomyrmex*, *aequalis* Mann and *simillimus* (Donisthorpe), can be said to possess this character, but in these the cephalic sculpturing is really a dense, fine rugoreticulum, and the striae of the first gastric tergite are much obscured by a dense puncturation, neither of which particulars are mentioned by Emery with reference to *vermiculatus.*

### Diacamma Mayr

*Key to the species, based on the worker caste*[1]

1. Humeri distinctly angulate ..... *purpureum* (Fr. Smith)
   Humeri evenly rounded ..... 2
2. First gastric tergite smooth; dorsal surface of head either smooth or at most feebly striate ..... *bispinosum* (Le Guillou)
   First gastric tergite and dorsal surface of head moderately to coarsely striate ..... *rugosum* (Le Guillou)

### Diacamma bispinosum (Le Guillou)

*Ponera bispinosa* La Guillou, 1841, Ann. Soc. Ent. Fr., 10: 317, worker. Type locality: Ternate.

*Diacamma bispinosum,* Emery, 1887, Ann. Mus. Stor. Nat. Genova, 4: 441. *Idem,* 1897, Rend. Accad. Sci. Bologna, p. 152, fig. 1, worker.

[1] Exclusive of *D. cupreum* (Fr. Smith), known certainly only from the type collection from Netherlands New Guinea.

*Diacamma bispinosa* var. *subsulcata* Emery, 1897, *ibid.*, p. 152, worker. Type locality: Halmahera. NEW SYNONYMY (provisional).

*Diacamma rugosum* subsp. *buruensis* Karawajew, 1925, Konowia, 4: 117-118, worker. Type locality: Tifu, Buru. *Idem*, 1935, Treubia, 15: 70, worker. NEW SYNONYMY (provisional).

Known only from the Moluccas.

The author was unable to locate the type of *bispinosum* during a visit to the Muséum National d'Histoire Naturelle, Paris, in 1955, and it may no longer be in existence. In the key I have followed the diagnosis of the species given by Emery in his 1897 revision of *Diacamma*. Emery's var. *subsulcata* is based on workers differing from the typical form only in possessing feeble striae on the dorsal surface of the head. Karawajew described his form *buruensis* with reference to *D. rugosum* alone, apparently unaware of the existence of *bispinosum;* his description fits the latter species well in diagnostic sculptural characters.

### Diacamma cupreum (Fr. Smith)

*Ponera cuprea* Fr. Smith, 1860, Jour. Linn. Soc. Zool., 5: 104-105, worker. Type locality: Dory (= Manokwari), Neth. New Guinea.

*Diacamma rugosum* var. *cuprea*, Emery, 1897, Rend. Accad. Sci. Bologna, p. 160, worker.

*Diacamma cupreum*, Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 462, worker.

Emery (1897) considered this form a trivial variant of *Diacamma rugosum*, differing from the typical form only in minor sculptural characters. However, Donisthorpe (1932) states that the type of *cupreum* is quite different from that of *sculpturatum* (an undoubted synonymy of *rugosum*): "In my opinion this species has nothing to do with *sculpturatum*, which is a much larger insect; the striae on the mesonotum [propodeum?—E. O. W.] are quite different and the gaster much smoother."

### Diacamma purpureum (Fr. Smith)

*Ponera purpurea* Fr. Smith, 1863, Jour. Linn. Soc. Zool., 7: 18, worker. Type locality: Halmahera.

*Diacamma rugosum* var. *purpureum*, Emery, 1887, Ann. Mus. Stor. Nat. Genova, (2)5: 439.

*Diacamma purpureum*, Emery, 1897, Mem. R. Accad. Sci. Bologna, p. 152, worker, distribution.

Known only from Halmahera, Moluccas.

### Diacamma rugosum (Le Guillou)

*Ponera rugosum* Le Guillou, 1841, Ann. Soc. Ent. Fr., 10: 318, worker. Type locality: Borneo. Emery, 1897, Mem. R. Accad. Sci. Bologna, p. 153, figs. 2-15, worker. (Holotype examined — Paris Museum.)

*Ponera sculpturata* Fr. Smith, 1859, Jour. Linn. Soc. Zool., pp. 142-143, worker. Type locality: Aru. (Holotype examined — Oxford University Museum.) NEW SYNONYMY.

*Diacamma rugosum* subsp. *sculpturatum*, Emery, 1897, *op. cit.*, p. 159, worker. Karawajew, 1926, Treubia, 8: 417, fig. 1, male. Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 454. Karawajew, 1935, Treubia, 15: 65, worker, male.

*Ponera vagans* Fr. Smith, 1960, Jour. Linn. Soc. Zool., 5: 103-104, worker. Type locality: Batjan. NEW SYNONYMY (provisional).

*Diacamma rugosum* var. *vagans*, Mayr, 1867, Tijdschr. Ent., 10: 55.

*Diacamma rugosum sculptum* var. *vagans*, Emery, 1897, *op. cit.*, p. 165.

*Ponera striata* Fr. Smith, 1860, *op. cit.*, p. 104, worker. Type locality: Batjan. Viehmeyer, 1912, Abh. Zool.-anthrop.-ethn. Mus. Dresden. 14: 6, note on type workers. NEW SYNONYMY (provisional).

*Diacamma rugosum* subsp. *striatum*, Donisthorpe, 1932, *op. cit.*, pp. 461-462. 1941, Trans. Roy. Ent. Soc. London, 91: 52, worker.

*Ponera tortuolosa* Fr. Smith, 1863, Jour. Linn. Soc. Zool., 7: 18, worker, queen. Original localities: Ceram, Buru. Nec *P. tortuolosum* Fr. Smith, 1858. (See *Diacamma rugosa* subsp. *smithi* Donisthorpe.)

*Diacamma rugosum* subsp. *tortuolosum*, Emery, 1897, *op. cit.*, p. 160.

*Diacamma rugosum sculpturatum* var. *divergens* Emery, 1897, *op. cit.*, p. 160, worker. Original localities: Halmahera, New Guinea. (Syntype examined — Emery Coll.) NEW SYNONYMY.

*Diacamma rugosum* subsp. *geminatum* Emery, 1897, *op. cit.*, p. 161, fig. 6, worker. Type locality: Halmahera. NEW SYNONYMY (provisional).

*Diacamma vagans* var. *papuanum* Stitz, 1911, Sitzber. Ges. Naturf. Freunde Berlin, p. 354, fig. 5, worker. Original localities: Mawa River, Neth. New Guinea; N-E. New Guinea. NEW SYNONYMY (provisional).

*Diacamma vagans* var. *frontalis* Stitz, 1911, *op. cit.*, p. 355, worker. Type locality: New Guinea. NEW SYNONYMY (provisional).

*Diacamma rugosum sculpturatum* var. *macreta* Viehmeyer, 1912, Abh. Zool.-anthrop.-ethn. Mus. Dresden, 14: 6, worker. Type locality Torricelli Mts., 640 m., N-E. New Guinea. NEW SYNONYMY (provisional).

*Diacamma bispinosum* var. *saussurei* Forel, 1922, Rev. Suisse Zool., 30: 89, worker. Type locality: Halmahera. NEW SYNONYMY (provisional).

*Diacamma rugosum sculpturatum* var. *pulchellum* Santschi, 1932, Mém. Mus. Nat. Hist. Belg. (hors ser.), 4(5): 12-13, fig. 1, worker. Type locality: Lomire, Neth. New Guinea. NEW SYNONYMY (provisional).

*Diacamma rugosum geometricum*, Karawajew, 1935, Treubia, 15: 62, worker.

*Diacamma rugosum sculpturatum* var. *papuana* Karawajew, 1935, *ibid.*, p. 67, worker. Type locality: New Guinea. *Nec Diacamma papuana* Stitz, 1911.

*Diacamma rugosum* subsp. *japensis* Donisthorpe, 1941, Trans. Roy. Ent. Soc. London, 91: 52, worker. Type locality: Mt. Baduri, 300 m., Japen I., Neth. New Guinea. NEW SYNONYMY (provisional).

*Diacamma rugosa* subsp. *smithi* Donisthorpe, 1943, Proc. Roy. Ent. Soc. London, (B)12: 115. Nom. pro *Ponera tortuolosa* Fr. Smith, 1863, *nec Ponera tortuolosa* Fr. Smith, 1858. NEW SYNONYMY (provisional).

*Material examined.* NETH. NEW GUINEA: Maffin Bay (6 nest series, E. S. Ross); Hollandia, 100 m. (J. L. Gressitt). N-E. NEW GUINEA: Nadzab (Wilson, nos. 1098, 1107); Lae (N. L. H. Krauss); Didiman Creek, Lae (Wilson, no. 692); Bubia (Wilson, nos. 681, 1069); lower Busu River (Wilson, nos. 992, 1008, 1020); Boana, 930 m., Bumbok Valley (Wilson, no. 1123); Goroka, 1550 m. (Gressitt); Kumur, 1000 m., upper Jimmi Valley (Gressitt); Sattelberg-Maroruo, 800-900 m. (Wilson, no. 724); Bolingbangeng-Nganduo, 900-1000 m. (Wilson, no. 731); Zingzingu, 1100 m. (Wilson, no. 766); Gemeheng, 1200-1300 m. (Wilson, no. 780); Sambeang, 400 m. (Wilson, no. 864). PAPUA: Mafulu, 1200 m. (L. E. Cheesman); Karema, Brown R. (Wilson, no. 553); Bisianumu, 500 m. (Wilson, nos. 618, 659, 669). ARU: (*sculpturatum* holotype).

*Taxonomic notes.* The unique worker type of *Ponera rugosa* Le Guillou was examined during a recent visit to the Muséum National d'Histoire Naturelle, Paris, and compared directly with a series from the lower Busu River, New Guinea (acc. no. 1020). The two are nearly identical, differing only in certain details of sculpturing that are undoubtedly part of the normal infraspecific variation; e.g., the type has 22 longitudinal striae between the compound eyes as opposed to 20 in the Busu River series. The Busu River series also compared closely with the worker type of *Ponera sculpturata* Fr. Smith in the Oxford University Museum.

In the author's opinion all of the Melanesian material cited in the preceding section, plus a large amount of additional Indo-Malayan material currently arranged under various varietal names of *rugosum* in the Museum of Comparative Zoology, belong to the single species *rugosum*. All of the Papuan-Moluccan forms listed in the synonymy are based on what appear to be nothing more than morphic or continuous variants, mostly in body sculpturing and size and form of the petiolar spines. Nevertheless, except in the two cases (*sculpturatum, divergens*) where I have seen type material, I have qualified the synonymy as provisional, since the existence of the closely related species *bispinosum* (Le Guillou) and *purpureum* (Fr. Smith) in the Moluccas suggests the possibility of the existence in New Guinea of still other sibling species that may fortuitously fit the types of one or more of the described forms.

A detailed description of variation in the Papuan-Moluccan population will not be attempted here. For an account of the extreme range of variation, particularly in body sculpturing, the reader is referred to Emery's detailed 1897 revision of *Diacamma* and subsequent descriptions of infraspecific forms by various authors.

*Ecological notes.* In New Guinea *rugosum* is abundant in both primary and second-growth rain forest over a wide range of elevation. At Nadzab a small colony, consisting of 20 to 25 workers and a quantity of brood in all stages of development from small larva to pupa, was found nesting in a shallow hollow in the side of a tree trunk about two meters from the ground. The ants had completely roofed over the hollow with a thin layer of vegetable debris and soil. At Didiman Creek another small colony was found nesting in a crack in a tree trunk at a point, about two meters from the ground, where the trunk had been snapped but not completely severed. The crevice, which ran horizontally into the fallen upper part of the trunk, had been filled in with vegetable debris and soil by the ants.

Workers of *rugosum* were commonly encountered during the day foraging singly on low vegetation and the trunks of trees. They were occasionally collected from as high as six meters in the tops of small, C-stratum trees but were never found in the

tops of recently felled, large, A-stratum trees. At the same time they were seldom encountered on the ground. The following prey record was made at the Busu River: a worker was collected as it was running up a tree trunk with a scolytid beetle in its mandibles. At Zingzingu workers were observed seemingly in the act of attending extrafloral nectaries on low herbaceous vegetation.

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# A NEW SPECIES OF CHELID TURTLE, PHRYNOPS (BATRACHEMYS) DAHLI, FROM COLOMBIA

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# A NEW SPECIES OF CHELID TURTLE, PHRYNOPS (BATRACHEMYS) DAHLI, FROM COLOMBIA

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No. 5 — *A New Species of Chelid Turtle,* Phrynops (Batrachemys) dahli, *from Colombia*

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During the summer of 1956 the senior author received from Dr. Fred Medem in Colombia a turtle for identification. The specimen could readily be identified as a member of the genus *Batrachemys* Stejneger, 1909, but was clearly different from the presently recognized species, *B. nasuta* (Schweigger, 1812).

Since Dr. Ernest E. Williams of the Museum of Comparative Zoology at Harvard University and Dr. P. E. Vanzolini of the Departamento de Zoologia da Secretario da Agricultura, São Paulo, Brazil, are currently collaborating in a revision of the South American members of the family Chelidae, these colleagues were at once advised of the new material from Colombia. In the meantime Dr. Williams gathered for study from various major collections as much material of this family as was possible. His comparisons soon indicated that the genera *Phrynops*, *Mesoclemmys* and *Batrachemys* were not as sharply distinct as the genera *Chelus*, *Hydromedusa* and *Platemys*, and there were notable difficulties at the species level as well. Dr. Williams felt that a direct discussion in the presence of the specimens might be useful and thus kindly invited the senior author to visit him at the Museum of Comparative Zoology during August, 1957. The results of this conference will be mentioned here only to the extent necessary for the present purposes and will be fully discussed in the forthcoming revision by Williams and Vanzolini.

There can be no doubt that the members of the three genera, *Phrynops, Batrachemys* and *Mesoclemmys* are very closely re-

lated forms — so closely related, in fact, that their inclusion in one genus, *Phrynops* Wagler, 1830, seems well justified. On the other hand, there are consistent minor features by which the three species groups can be separated. Accordingly, the announced revision will recognize the three groups as subgenera.

Boulenger (1889) illustrated the skulls of *Batrachemys nasuta* and *Phrynops hilarii*. Both represent large specimens. The differences between these skulls are most notable in that the parietal crest is very narrow, and the parieto-squamosal arch extends far behind the exoccipital region of the skull in *Batrachemys;* in *Phrynops* the parietal crest is broad and the parieto-squamosal arch lies dorsal and slightly anterior to the exoccipital bone. The material presently assembled at the Museum of Comparative Zoology shows that these differences are not quite as striking, if one compares skulls of juvenile as well as adult specimens of these with other species of *Phrynops* or of *Mesoclemmys*. Skulls of juvenile individuals, particularly, show much greater similarity than do those of old specimens, which is, of course, not especially surprising. The two conditions as outlined above, can be clearly distinguished on X-ray plates, much better, we think, than on the actual skulls, because the skulls often are injured or slightly warped in maceration so that the exact position and nature of the parieto-squamosal bar is difficult to ascertain.

A more complete characterization of these three subgenera of the genus *Phrynops* is immaterial for the present description of a new species and will be given in the revision mentioned above.

## Order Testudinata

### Suborder Pleurodira

### Family Chelidae

### Genus Phrynops Wagler

### Subgenus Batrachemys Stejneger

### Phrynops (Batrachemys) dahli,[1] sp. nov.

*Holotype:* adult male, CNHM 75980.

*Paratypes:* an adult female, CNHM 81991; a juvenile male, CNHM 81992; a hatchling, CNHM 81993.

[1] Named in honor of Prof. George Dahl of the Liceo Bolivar in Sincelejo, who collected the material and brought it to the attention of the junior author.

*Locality:* Vicinity of Sincelejo, Bolivar, Colombia.

*Local names:* The turtle is evidently well known to the people of the middle and upper Sinú valley under the name "Carranchina."

Up to the present, only one species of *Batrachemys* has been recognized by the reviewers of the group, Boulenger (1889), Siebenrock (1909), and Mertens and Wermuth (1955): *B. nasuta* (Schweigger). However, the collections presently assembled by Dr. Williams clearly suggest that there are several species represented, even though some vast areas, such as the Amazon Basin, have not yet yielded sufficient material to permit adequate conclusions. *B. tuberculata* (Luederwaldt, 1926), distributed throughout the drainage area of the Rio San Francisco, is now well represented by a large series of specimens, and is quite distinct from *B. nasuta.* The material from Colombia, described below, is likewise quite distinct. A very few specimens, from distant points in the Amazon drainage and elsewhere seem to indicate that other species besides *B. nasuta* will be recognizable when additional material from these areas becomes available.

*Diagnosis:* Plastron narrow, especially across posterior lobe; particularly pronounced in males. Limbs powerful; feet large and strongly webbed. Skin of neck lacking tubercles. Carapace olive-brown above, yellow below. Plastron and bridge bright yellow with shield boundaries outlined in gray. Head a fairly uniform gray dorsally, bright yellow or whitish below, including the angle of the mouth and the tympanic membrane. A fine bluish-gray streak extends from nose to anterior corner of eye and from posterior rim of eye-socket to dorsal edge of tympanic membrane and along the side of the neck, forming boundary between gray and whitish skin areas. Color of hatchling much as in adult, but shield boundaries more sharply outlined in dark gray, and whitish underside of head and neck with a few small gray specks and dots.

*Description: External features.* The series of specimens at hand is small, but probably adequate to characterize the species, since there are few noteworthy differences between the specimens, which present a rather uniform appearance.

The carapace of this species is characteristically tapered in dorsal aspect, widest at the 7th marginal pair of scutes, narrowing to about the second (Pls. 1, 2). Between the marginals mentioned the edge of the carapace is slightly curled upward. In the area of the second, third and fourth vertebral shields the shell is slightly flattened, sometimes even a little depressed, and provided with a weak carina in the juveniles; in the adults the keel is interrupted and, at least in CNHM 75980, barely noticeable. In the type specimen the costal plates are more strongly curved than in the juvenile or in the female.

Figure 1. Graph to illustrate the relative width of the posterior lobe of the plastron in *Phrynops* (*Batrachemys*) *dahli*, *P.* (*B.*) *nasuta* and *P.* (*B.*) *tuberculata*. The indices were calculated as follows: width of posterior lobe at base times 100 divided by total length of the plastron.

The plastron is very narrow in this form. In the type, in the juvenile male, and in the hatchling, the width of the posterior plastral lobe amounts to only 36 to 38 per cent of the total length of the plastron (see Fig. 1). In the female, CNHM 81991, the plastron as a whole is somewhat wider, the width of the posterior lobe reaching 42 per cent of the plastral length. Greater plastral width in females than in males was observed in other species of this family and may reflect sexual dimorphism. The anterior

plastral lobe, always wider than the posterior lobe, is broadly rounded in front with the wide intergular slightly protruding. The posterior lobe is deeply notched behind.

The head is covered, dorsally, with very smooth skin, traversed by a system of extremely fine skin furrows that subdivide the upper head region into numerous irregular polygons of different size, thus simulating true scutellation. The skin of the underside of the head and of the neck shows normal papillation but there are no traces of horny tubercles. In the adult male the papillation is particularly well developed below the chin.

The limbs are notably larger in the male than in the female of nearly equal size. The forelimb is distally expanded to form a relatively large paddle, the surface of which is further increased by a row of much enlarged scales along the ulnar edge of the limb, forming a scale fringe from the stylopodial region all the way to the claw of the fifth digit. The hind feet are provided with a series of four keeled and much enlarged scales along the tibial edge of the zeugopodium. The pes is heavily webbed with the fifth digit, which does not bear a claw, supporting the large fringe of webbing along the outer side of the foot.

In the female the tail is very short, tapering rapidly to a fairly sharp point. The cloacal opening lies within the fork of the plastral lobe. In the male the tail is much larger; the cloacal opening lies some distance behind the tips of the plastral fork. The tail region behind the cloacal opening is short and tapers sharply to a point. On the underside of the cloacal region the scalation (or rather papillation) of the skin is coarser than on the sides or top.

*Color pattern:* Besides fairly fresh specimens preserved in alcohol, the junior author has provided good color photographs of live specimens. The carapace is covered dorsally with rather translucent [1] (thus lightly pigmented) uniformly dull olive-brown shields. The lower sides of the marginal shields are bright yellow with the edges between adjacent scales outlined in dark gray. The plastron, and the bridges likewise, are yellow or whitish-yellow with the shield boundaries outlined in gray. In

[1] The sutures between the underlying bony plates are clearly visible through the epidermal shields when the specimens are wet.

the female specimen, CNHM 81991, the underside of the marginals, the bridge and the plastron are irregularly mottled with brown. Examination under the binocular microscope shows that the brown areas are not part of a color pattern; they are confined to superficial, horny flakes that were in process of being shed by the animal at the time of death. Most of these flakes are loose and can readily be removed. There is no brown pigment below these flakes. This seems to indicate that the brown color is the result of staining of the horny surface by an agent present in the particular environment in which this individual lived.

The dorsal side of the head is a fairly uniform gray that extends to the nostrils, laterally to the upper edge of the horny beak and from there to the dorsal rim of the tympanic membrane. On either side, a narrow bluish-gray streak runs from the nostril to the anterior corner of the eye and from the posteriormost point of the rim of the eye to the dorsal edge of the tympanic membrane. From here it extends backwards along the side of the neck separating the dark gray upper side of the neck from the yellow or whitish underside. The horny beaks, both upper and lower, are yellow. The angle of the mouth and the entire tympanic membrane lie in the yellow or whitish territory of the underside of the head. In the hatchling the color pattern is much as in the adults, except that the underside of head and neck shows a number of small but distinct gray specks and dots. The limbs and the tail are generally dark gray above and whitish, mottled with light gray, below. In the female specimen, CNHM 81991, the underside of the hindlimbs has a reddish cast. Examination reveals that this, like the brown mottling on the plastron (see above) is a stain affecting the surface of the horny scales only.

*Skeleton:* The skeleton, except for the skull, was studied from X-ray plates only. Stereoscopic X-ray plates were made of the type specimen, before the skull was removed. Simple dorsoventral X-rays served for CNHM 81991 and 81992. These X-ray plates were compared with plates of *Phrynops* (*Batrachemys*) *tuberculata* as well as with a number of other members of this genus.

The skull is illustrated in Figures 2-4. It is very large relative to the size of the animal, its total length being about 30 per cent of the straight length of the carapace in the adult, about 45 per cent of that length in the hatchling (see Pl. 2).

The skull (Figs. 2-4) shows all the typical features of that of *Phrynops* (*Batrachemys*) *nasuta* as pictured by Boulenger (1889). The differences are probably due, to some extent, to the fact that Boulenger's specimen was a very old and large individual, and some of the sutures may not have been visible (as

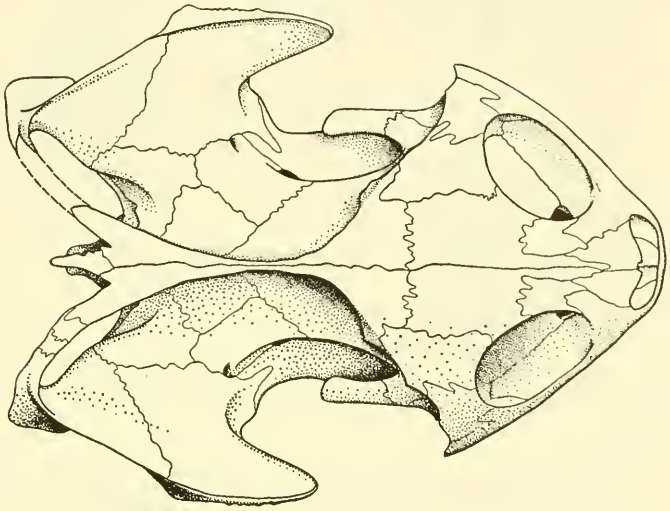

Figure 2. Skull of *Phrynops* (*Batrachemys*) *dahli* type specimen. Dorsal view.

for example the suture between opisthotic and supraoccipital); also there are differences in proportion, the skull of the Colombian species being notably more pointed anteriorly — which may or may not be a specific character. In *dahli* the maxillary rim lateral to the orbit is relatively narrower than in *nasuta* and the suture between opisthotic and squamosal on the dorsal side of the otic region of the skull reaches much farther mediad than in the compared species. The basisphenoid of *dahli* is short,

lacking the slender anterior prong seen in *nasuta* and the pterygoids lack anterior processes on either side of the vomer. In *dahli*, furthermore, the premaxillae are almost in contact, ventrally, with the vomer.

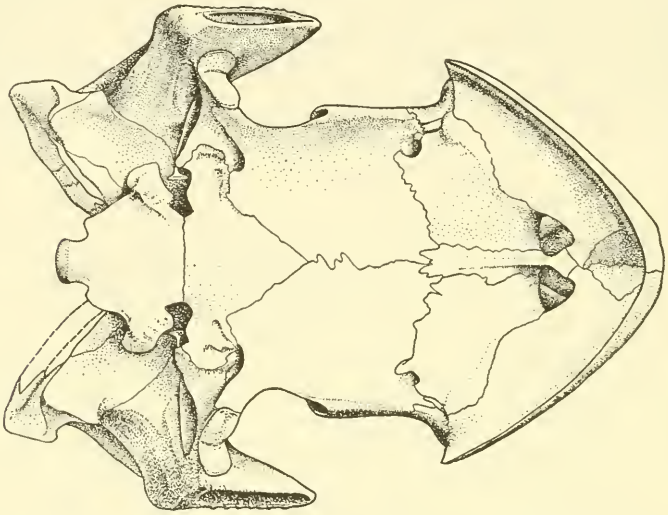

Figure 3. Skull of *Phrynops* (*Batrachemys*) *dahli* type specimen. Ventral view.

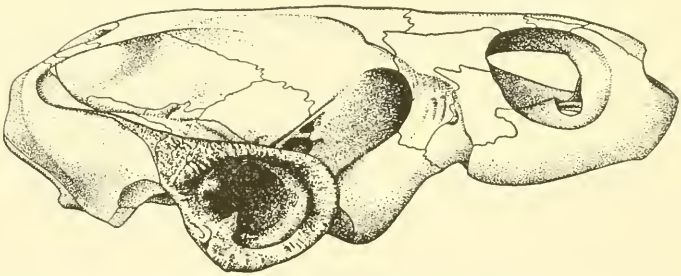

Figure 4. Skull of *Phrynops* (*Batrachemys*) *dahli* type specimen. Lateral view.

The skull of the type specimen (Fig. 2) shows an interesting abnormality. The extremely thin posttemporal bar, normally formed to about equal measure by the parietals and the squamosals, includes two supernumerary bones on the right side; on the left side the bar was injured, but since the remaining prongs of the bar are the sutural ends of the parietal and squamosal bones we must assume that the abnormal condition was paired.

The hyoid apparatus is well ossified and complex (Fig. 5). The hyoid body consists anteriorly of two pairs of bones and

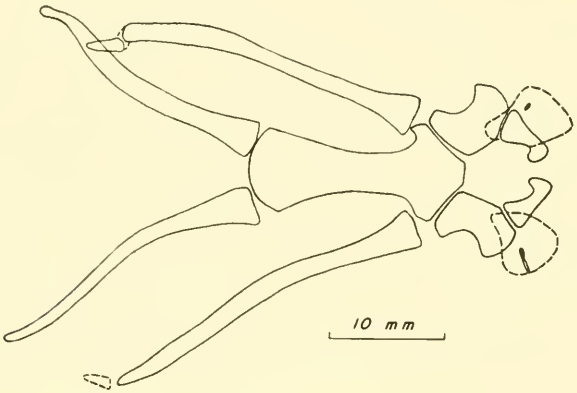


Figure 5. Hyoid apparatus of *Phrynops* (*Batrachemys*) *dahli* type specimen, drawn from X-ray plate.

posteriorly of an elongated unpaired element thus evidently ossifying from five distinct centers as noted by Siebenrock (1899). As in other forms (for example in *Clemmys*), there is a pair of cartilages associated with the anterolateral part of the hyoid body, that has been identified as reduced hyoid horns (Romer, 1956, p. 421). The cornua branchialia I are attached to the complex copula where the second pair of elements join the unpaired plate. The distal tips of these branchial horns seem to have separately ossified (or calcified — a definite identification

is not possible in the X-ray) terminal elements. The second pair of cornua branchialia originate in the usual fashion from the posterior end of the copula, but here this portion of the hyoid body is broadly rounded, rather than forked as in *Clemmys* or *Trionyx*.

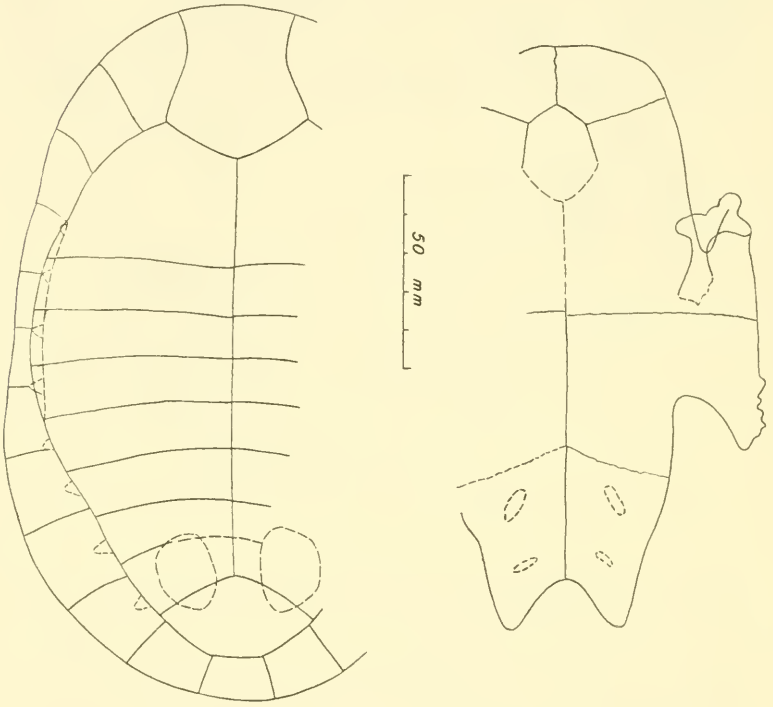


Figure 6. Carapace and plastron of *Phrynops* (*Batrachemys*) *dahli* type specimen, drawn from stereoscopic X-ray plates.

The carapace (Fig. 6), typically elongated in the anterior region as in all pleurodires, shows a complete lack of neural plates, at least in the type specimen, CNHM 75980 and in

CNHM 81992. In CNHM 81991 no neural plates were observed in the X-ray, but in the critical area, between the first costal plates, the picture is difficult to interpret. Since Figure 6 was drawn from X-ray plates, it includes features that would not ordinarily be visible on the macerated shell (for example the distal rib ends) or would not be visible from one aspect of the shell only — such as the internal ilial scars of the carapace, the ventral rim of peripherals 4 to 7, the pelvic scars on the plastron and the buttress pillars.

In the type specimen and in CNHM 81991 the carapace is solidly ossified. In the juvenile, CNHM 81992 with a carapace length of 112 mm., a costoperipheral fontanelle extends from the third to the eighth peripheral. In this same specimen, on the right side, there is a supernumerary peripheral.

The plastron is attached to the carapace by a powerful anterior buttress pillar only. In both adult specimens the bridge suture remains open and there is no indication of a posterior buttress. In the juvenile a lateral fontanelle marks the immature state of ossification. The buttress pillar is shown in the plastron figure (Fig. 6), and consists of an anterodorsal extension for the attachment to the carapace and a posteroventral attachment to the plastron.

The posterior outline of the entoplastron could not be made out on the X-ray. This indicates that the suture, instead of being vertical, is strongly oblique in that area and thus failed to produce a sharp suture shadow.[1]

The vertebral column of the neck shows the central articulation pattern indicated by Williams (1950) for the chelid turtles. In the juvenile specimen the joint between vertebral bodies 7 and 8, however, seems incompletely developed; instead of a concave surface on centrum 7 and a convex one on centrum 8, both are flat. Little can be said about the shell vertebrae from what is visible in X-ray pictures. However, the oval opening formed by the

[1] Oblique entoplastral sutures are known in many turtles and this accounts for the fact that the dorsal and ventral outlines of the entoplastra differ from each other notably.

posterior edge of the first (vestigial) shell rib and the anterior edge of the second is always clearly visible. It is rather large in this species (see below). There are (in the present material) constantly 17 tail vertebrae. In the female which has a considerably shorter tail, the vertebrae are smaller and more feebly developed.

In the shoulder girdle the coracoid is but moderately expanded distally. Humerus and zeugopodium show no peculiarities. The carpus consists of radiale, intermedium, ulnare and five distal carpals. No centralia were noted. In the hand the third ray is the longest, the fifth the weakest.

The pelvis is not clearly enough visible in the pictures to permit description. The tarsus consists of tibiale, intermedium and fibulare proximally and of five distal tarsals of notably uneven size. The fifth is the largest and permits the fifth digit of the pes to be spread away from the fourth. The second and third digits are the longest and of nearly equal length. The fifth has a much reduced terminal phalanx that does not have a claw and the entire digit is fairly long and slender.

*Food:* No field observations exist concerning the food preferences of this species. But the X-rays of some specimens show abundant stomach and intestinal content. Most of this is in the form of mashed, compact food masses that do not permit recognition of the nature of the food. In one specimen, CNHM 81991, however, there are some broken splinters of long bones with very thin walls. Unfortunately, the ends of these bones are not visible, thus rendering further identification impossible.

*Comparisons:* Full comparison is possible between the present species and the adequately known *Phrynops* (*Batrachemys*) *tuberculata*. The type species *nasuta* of the subgenus *Batrachemys* is not at present a clearly definable entity due to insufficient representation and this makes comparison with the Colombian species unsatisfactory.

Externally the Colombian species differs from *tuberculata* by the lack of horny tubercles on the neck, by the uniformly yellowish or whitish plastron which is always a yellowish-brown ground color variously marked with dark brown blotches in *tuberculata*.

The lower side of the neck in the latter is usually dark gray, variously mottled with yellowish-brown, but lightly colored specimens occur in which the carapace, plastron, and the underside of the neck are fairly uniform yellowish-brown, lacking dark brown or dark gray mottling. As regards proportions, the Colombian species has, at all age levels, a relatively much more narrow plastron than does *tuberculata;* this is particularly striking in the posterior plastral lobe (see Fig. 1). In the skeleton the two species differ in the distal expansion of the coracoid which is consistently greater in *tuberculata* than in *dahli;* in the absence of a well-defined posterior plastral buttress in *dahli;* in a slightly larger opening between the two anteriormost shell ribs in *dahli;* in the size of metatarsals IV and V which are relatively longer and more slender in *dahli.*

Comparisons with *nasuta* are at present restricted to external features. In specimens referred to this species from the eastern end of the Amazon drainage (Para, Brazil) the carapace is a dull gray-brown. In juveniles, however, there are light brown, angular areas on the dorsal sides of the lateral marginal scutes (Nos. 3-9) and the ventral faces of all the marginals may be bright yellow. The plastron is dull brownish all over, possibly with yellow fringes along the anterolateral and posterolateral edges; in juveniles the central area of the plastron is dark brown, fringed with bright yellow all around except, perhaps, on the intergular. Head and neck are dull gray-brown above and below except for a yellow or whitish band along the ventral side of the mandible; in the juvenile there is furthermore an oblong, yellow mark over the temporal region and extending, less sharply defined, forward to the tip of the nose. One adult individual shows this pattern faintly. The limbs seem to be more feeble than in *dahli* or *tuberculata.* The color pattern of this form is quite characteristic and very notably different from that of the Colombian species.

A juvenile specimen, possibly representing a geographic race of *nasuta,* from the opposite side of the Amazon drainage (eastern Bolivia) differs greatly from the Para material. It has a

light brown carapace with yellow marginals beneath, whose shield boundaries are marked by brown edges. The plastron is light brown with yellowish fringes posterolaterally. The limbs are gray except for yellow areas beneath the thigh. The neck is dull brown above, throat and neck brown below. The mandible, the maxillary beak and the tympanic membrane are whitish. The dorsal surface of the head is light brown with a mottled pattern of darker brown spots. The color pattern of this specimen differs from that of *dahli* primarily in the brown underside of throat and neck and the plastral pigmentation. *Emys barbatula* Gravenhorst (1829), *Hydraspis raniceps* Gray (1855) and *Hydraspis maculata* Gray (1873) are based on specimens that resemble fairly closely the materials from the eastern end of the Amazon Basin, described above.

*Distribution and Habitat:* The present species is documented by specimens from the area of Sincelejo only. The only clue as to its probable distribution lies in the fact that the people of the middle and upper Sinú valley know the animal by name (see above), considering it as not edible. The turtle does not live in the major rivers, such as the Sinú or the Betanci, or in the lagunas, but rather prefers ponds in the woods. It is a fast walker on ground and may be found long distances from water. Nothing is recorded concerning its behavior in the water.

*Acknowledgements:* The writers are greatly indebted to Dr. Ernest E. Williams of the Museum of Comparative Zoology at Harvard University, who has kindly invited the senior author to look at the results of his and Dr. Vanzolini's forthcoming revision of the South American members of the family Chelidae thus providing a far better background for the present description than would have been otherwise possible. Our sincere thanks are due also to Dr. Robert F. Inger and especially to the late Dr. K. P. Schmidt whose contagious enthusiasm and love of herpetology have greatly inspired both of us. Miss Maidi Wiebe, staff artist, Department of Geology of Chicago Natural History Museum, has rendered the illustrations in her meticulous and expert manner.

## MEASUREMENTS

*Phrynops (Batrachemys) dahli*, sp. nov.

| | CNHM 75980 type | CNHM 81991 | CNHM 81992 | CNHM 81993 (juv.) |
|---|---|---|---|---|
| Carapace length, horiz. | 184 mm. | 177 mm. | 112 mm. | 36.5 mm. |
| Carapace width, max. | 125 | 130 | 86 | 27.0 |
| Shell height | 57 | 54 | 34 | 12.5 |
| Carapace width at marginals 3-4 | 104 | 107 | 67 | 23.0 |
| Plastron length, max. | 160 | 155 | 99 | 29.0 |
| Plastron length to notch | 143 | 141 | 90 | 27.0 |
| Width anterior lobe, at base | 74 | 80 | 48 | 14.0 |
| Width posterior lobe, at base | 58 | 65 | 38 | 11.0 |
| Width across anal sulci | 44 | 47 | 29 | 7.4 |
| Bridge length | 37 | 37 | 24 | 6.0 |
| Head length | 53 | 52 | 37 | 16.0 |
| Head width, max. | 42 | 47 | 29 | 13.5 |

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# PLATES

Plate 1. *Phrynops* (*Batrachemys*) *dahli*, type specimen CNHM 75980, prior to removal of skull. The skin of the head had suffered partial decomposition during shipment. Dorsal and ventral views.

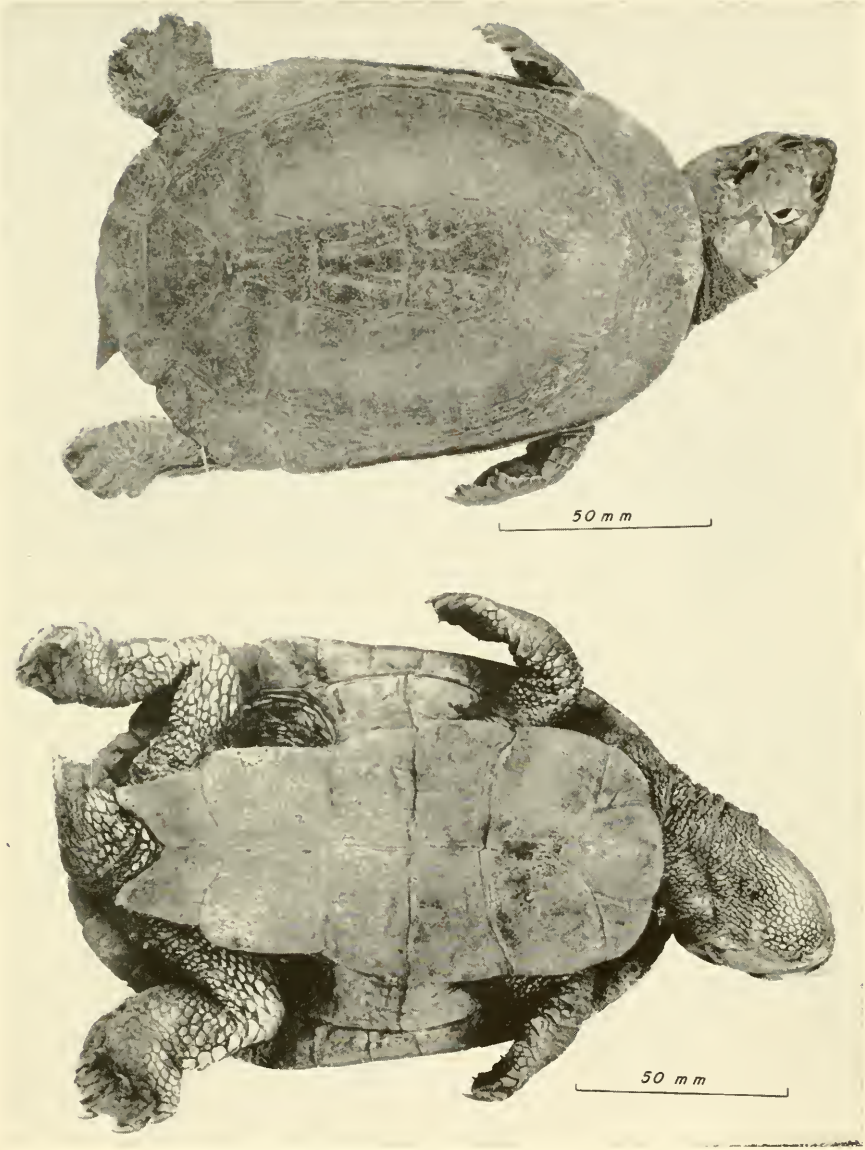


PLATE 1

Plate 2. Hatchling of *Phrynops (Batrachemys) dahli*, CNHM 81993. Dorsal and ventral views.

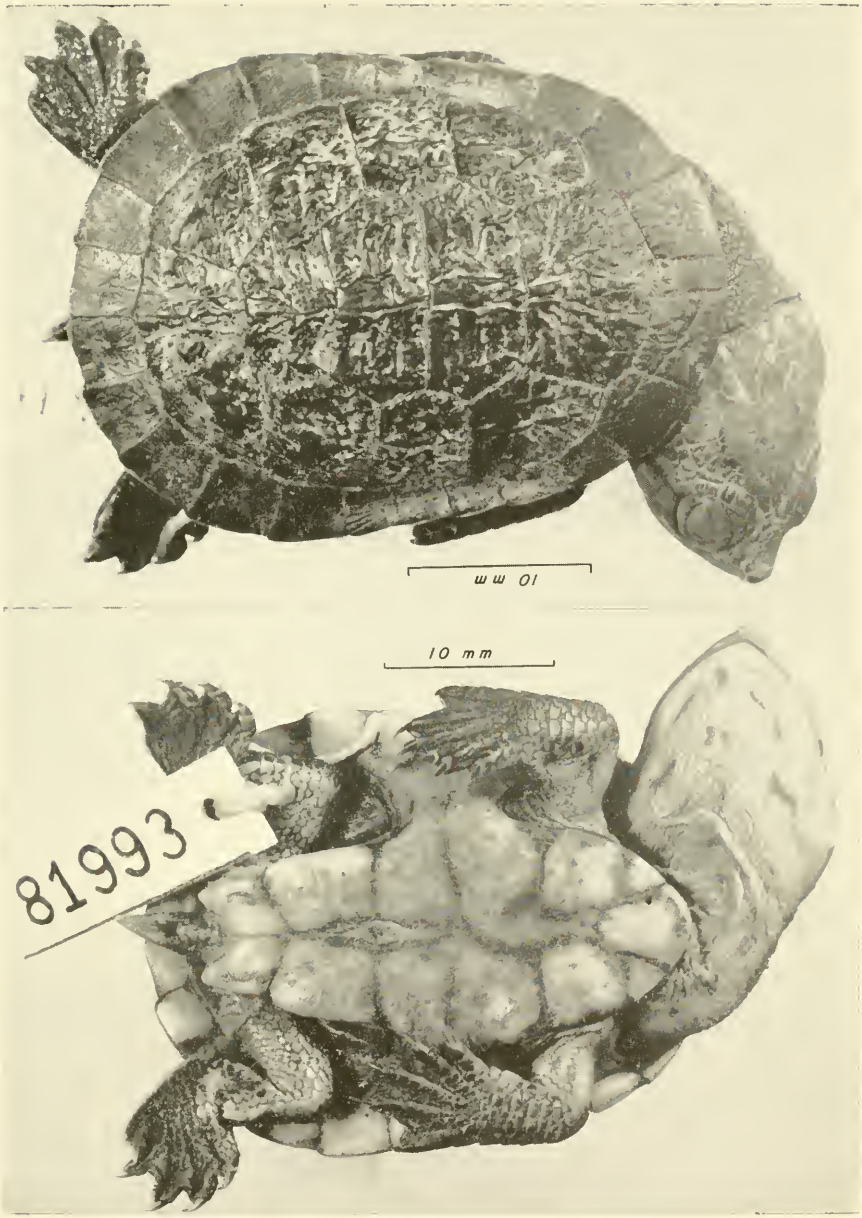


PLATE 2

Bulletin of the Museum of Comparative Zoology
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Vol. 119, No. 6

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# TARACTES ASPER AND THE SYSTEMATIC RELATIONSHIPS OF THE STEINEGERIIDAE AND TRACHYBERYCIDAE

By Giles W. Mead and G. E. Maul

With One Plate

PRINTED FOR THE MUSEUM
CAMBRIDGE, MASS., U. S. A.
October, 1958

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# No. 6 — Taractes asper *and the Systematic Relationships of the Steinegeriidae and Trachyberycidae*

By Giles W. Mead[1] and G. E. Maul[2]

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## INTRODUCTION

In an earlier paper one of us reviewed the status of certain species of bramid fishes (Mead, 1957). Excluded from that account were several nominal species related to *Taractes longipinnis* which were so poorly known that a comparison of them with the more common *Taractes* was impossible. This study is concerned principally with three such forms: *Taractes asper* Lowe, 1843, *Steinegeria rubescens* Jordan and Evermann, 1887, and *Trachyberyx barretoi* Roule, 1929.

Our study has indicated that the genus *Taractes* contains species of two distinct types, one with a deep body, the other with a less deep one. Two subgenera are recognized for these types: *T.* (*Taractichthys,* new), and *T.* (*Taractes*) respectively. We have also concluded that *Taractes asper* is not the juvenile of *Taractes longipinnis* as has customarily been assumed, but is a valid species of *Taractes* (*Taractes*), the adult of which is un-

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known. The series of specimens described by Maul from Madeira as *Trachyberyx barretoi* are considered identical with *Taractes* (*Taractes*) *asper*. Maul's fishes, which are questionably identified with Roule's type of *Trachyberyx barretoi* and on which Maul based the berycoid family *Trachyberycidae*, are not berycoids but bramids. We have also found that the juvenile fish described as *Steinegeria rubescens* (*Steinegeriidae*) is closely related to *Taractes* (*Taractes*) *asper*. An account of the relationships of these species and the nomenclatorial consequences of our classification follows below.

In addition to comparative bramid and berycoid specimens contained in the Museu Municipal do Funchal and the U. S. National Museum, our study material includes the following specimens:

The type of *Steinegeria rubescens*.

A juvenile *Steinegeria rubescens* from the Gulf of Mexico (United States Fish and Wildlife Service exploratory vessel *Oregon* station 1473: 24° 48′ N. Lat., 91° 40′ W. Long.; March 26, 1956; from the stomach of an *Alepisaurus ferox* which was caught on a tuna long-line).

An adult from the Gulf of Mexico about 200 miles south of Mississippi (caught on a tuna long-line by the commercial fishing vessel *Sirocco*).

An additional juvenile, tentatively referred to *T. rubescens*, from the Pacific off Upolu Point, Hawaii (taken by the U. S. Fish and Wildlife Service research vessel *Hugh M. Smith III*, April 17, 1950; from the stomach of a pelagic octopod, *Eledonella* sp., which in turn was taken from the stomach of an *Alepisaurus ferox*).

The series of Madeiran specimens which were discussed by Maul (1954:18) as *Trachyberyx barretoi* and additional juvenile specimens of the same species from Madeira.

We are indebted to the Curators of the Museum of Comparative Zoology, Harvard University, and the Natural History Museum, Stanford University, for making their specimens of bramid and berycoid fishes available to us. Several individuals have provided specimens or supplementary information, and we wish here to record our appreciation to Prof. Umberto d'Ancona, Istituto di Zoologia e Anatomia Comparata, Padova, Italy; Dr.

G. Belloc, Institut Océanographique, Monaco; and to Dr. Albert L. Tester, John W. Reintjes and Harvey R. Bullis, Jr., of the U. S. Fish and Wildlife Service.

## Taractes

In their careful study of a western North Atlantic *Taractes*, Bigelow and Schroeder (1929) separated the species of *Taractes* from *Brama* on the basis of the number of scales in a longitudinal series. They included seven nominal species within the genus: *T. asper* Lowe, *longipinnis* (Lowe), *brevorti* (Poey), *raschi* (Esmark), *princeps* Johnson, *saussuri* (Lunel) and *steindachneri* (Döderlein). These species, and the two which were described subsequently (*T. platycephalus* Matsubara and *T. miltonis* Whitley), were later reviewed by Mead (1957). In both of these papers *T. asper* was considered a dubious species but retained as distinct from its congeners. The results of the two studies differ principally in the treatment of *T. princeps* Johnson, which Bigelow and Schroeder thought had best be considered distinct from *T. longipinnis*, and *T. raschi*. *T. asper* will be discussed more fully below, and the specific differences, if any, between *T. princeps* and *T. longipinnis* will not affect our present understanding of *Taractes*. *T. raschi* is treated here as a distinct species.

The great changes in form of vertical fins, type of scalation and the like during growth has been troublesome to those who have attempted taxonomic studies of the bramids. A feature which separates these nine species into two natural groups is the relative depth of the body, and correlated with it the dorsal profile of the head. This is recognized here as a subgeneric characteristic, although a test of its validity must await the capture of full developmental series of each species.

The type figures of *Taractes raschi* (see Smitt *et al.*, 1892-95, fig. 24: Mead, 1957, fig. 4) and *T. platycephalus* (Matsubara, 1936) show shallow-bodied forms with concave foreheads. Measurements taken from Esmark's figure of *T. raschi* show that the greatest depth of body is contained 2.4 times in standard length, 2.7 in fork length, and about 3.1 in total length. These ratios for *T. platycephalus* are: 2.3, 2.8 and 2.9. (We will note below that the adult *Taractes rubescens* is in this shallow-bodied group.

The comparable depths in standard, fork and total length are: 2.5, 2.7 and 3.1. Our analysis of *T. asper* also suggests that its adult should be placed here.) We propose the subgenus *Taractes* (*Taractes*) for these four species.

Differing from this group are the adult *Taractes* which are more frequently caught (for example, those reported by Bigelow and Schroeder, 1929; Fitch, 1953:546; Whitley, 1938:191; Fowler, 1956). In these the foreheads are convex and steeply inclined; the fins, although variable, are more strongly falcate; and the general form is somewhat rhomboidal. In the deep-bodied Atlantic specimen reported as *T. princeps* by Bigelow and Schroeder (1929) the maximum depth is contained 1.9 in standard length, 2.1 in fork length and about 2.6 in total length. These measurements on smaller Atlantic deep-bodied specimens are: 1.6-2.0, 1.8-2.1 and 1.8-2.6. Published figures of *T. saussuri* Lunel, *T. steindachneri* Döderlein and *T. miltonis* Whitley identify these species with the deep-bodied forms. Poey's description of *T. brevorti* also defines a deep-bodied species.

Fortunately, Johnson recorded standard length as well as "total" length for one of his specimens of *T. princeps*. The body depth is contained 1.9 and about 2.6 in these lengths respectively, thus establishing his species as a deep-bodied form. Lowe (1843:82) was less precise in his original account of *T. longipinnis*, for he says only that, "The example seen measured eighteen inches and a quarter in length, and was eight inches deep at the origin of the dorsal and anal fins," a ratio of 2.28. If he was referring to standard length, *T. longipinnis* would be among the shallow-bodied species distinct from *T. princeps* and allied to *T. raschi*. Nowhere in his 1843 paper does he define "length" and, since there are no figures, a more definite meaning cannot be deduced from his account of other species there described. A perusal of his "Fishes of Madeira" (1843-60), however, has convinced us that Lowe's "length" refers to a total or overall length, since the two terms are used interchangeably in that publication and the morphometric ratios of the fishes there described and figured are given in terms of a total, not a fork or standard, length. *Taractes longipinnis* can thus be placed among the deep-bodied species, for the ratio 2.3 is within the range of other deep-bodied forms but not within that of the rarer less-deep species.

Within this second subgenus of *Taractes, T.* (*Taractichthys*), we therefore include these named deep-bodied forms: *longipinnis, brevorti, princeps, saussuri, steindachneri* and *miltonis.*

We can turn now to the three named species which are the principal concern of this paper: *Taractes asper, Steinegeria rubescens* and *Trachyberyx barretoi.*

## Taractes asper Lowe, 1843

Lowe based *T. asper* on a single "plain and sober-coloured little fish" from Madeira. One of us has searched the collections of the British Museum for this and other of Lowe's types, but could not find *T. asper.* Since we believe that this fish bears a close resemblance to those later described under the generic names *Steinegeria* and *Trachyberyx,* and since *T. asper* is the type species of *Taractes,* we quote here Lowe's original description of *Taractes* and *T. asper.* In the absence of a figure and of the type specimen, this description constitutes our entire knowledge of that species.

"Gen. *Taractes,* nob.

"*Char. Gen.* — *Corpus* ovatum compressum (ad finem pinnae dorsalis analisque abrupte in caudam contractum), squamis cycloideis retrorsum aculeato-umbonatis muricato-asperum. *Caput* squamosum; oculis magnis; rostro brevissimo simo; rictu magno subverticali; dentibus *Bramae* similibus subscobinatis recurvis, externis majoribus; palatinis vomereque armatis. *Operculum* simplex inerme. *Praeoperculum* basi eximie dentato s. subcalcarato; suboperculo interoperculoque denticulatis.

"*Pinnae* malacopterygiae, s. omnes radiis mollibus. *Ventrales* subjugulares. *Pinna dorsalis analisque* unica conformis lata; *caudalis* simplex integra rotundata. *Membrana branchiostega* septem-radiata.

"*Squamae* magnae trapeziformes postice emarginatae cycloideae; umbone in aculeum recurvato-erectum producto.

"*Taractes asper.*

D. 5 + 28; A. 3 + 20; P. 17; V. 1 + 5; C. $\frac{4 + \text{VIII}}{3 + \text{VII}}$; M. B. 7; Squamae corporis in serie longitudinali 43 fere.

"The generic name imposed at its first discovery on this particularly interesting, though plain and sober-coloured little fish, expresses the difficulty experienced in settling its relations of affinity, which are

indeed so obscure and complicated, that but for the subsequent discovery of *Brama longipinnis*, with its similarly, though contrariwise, hooked scales, its true position, next to *Brama*, with analogies to many other families (e.g. *Zeniclae, Caproidae, Scombridae*), must have remained in abeyance.''

Immediately above his account of *Taractes,* Lowe described a similar fish, *Brama longipinnis.* Later workers, for want of a better knowledge of *Taractes asper*, have considered this species to be a young stage of *T. longipinnis.* This practice is no longer

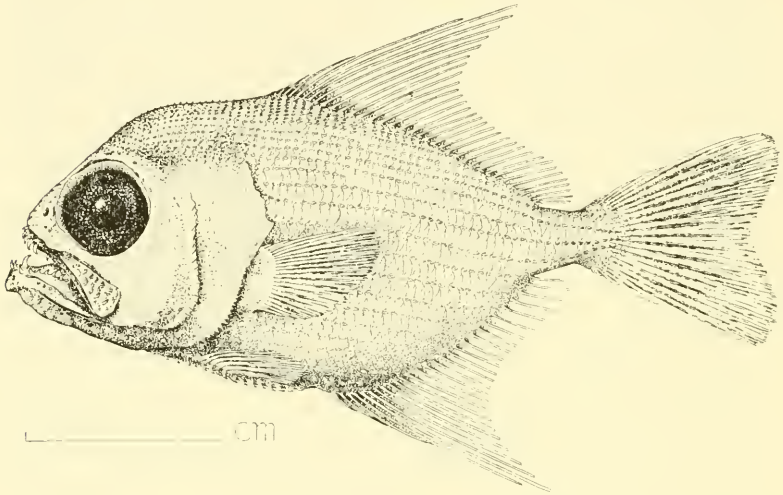


Figure 1. Juvenile *Taractes* (*Taractichthys*) *longipinnis,* about 30 mm. in standard length. (Museu Municipal specimen no. 345; drawn by G. E. Maul.)

appropriate. Mead (1957) has described a 74 mm. juvenile *Taractes longipinnis* (with which he considered *T. princeps* identical), and a 30 mm. fish which can best be referred to this species (Fig. 1) was collected by Maul at Madeira and is now in the Museu Municipal, Funchal. These juveniles, and the published descriptions of adults of various sizes (Barnard, 1948:374; Bigelow and Schroeder, 1929; Fitch, 1953:539; Whitley, 1938; etc.) differ in several aspects from Lowe's type description of *T. asper.* His fish was said to have a spine-bearing preoperculum,

uniformly broad dorsal and anal fins, and a simply rounded caudal fin. These are not attributes of the young of *Taractes longipinnis*, for the denticulations of the operculum and preoperculum of the young can hardly be called spines, both the dorsal and anal fins become falcate at a very small size, and the caudal fin changes from a simple fork in the young to the deeply concave, scombrid-like type of the adult. Nor is it likely that Lowe's *T. asper* is the young of one of the other bramid genera: *Brama*, *Collybus* or *Eumegistus*. We have seen the young of the first two of these and the juvenile *Brama leucotaenia* Fowler,

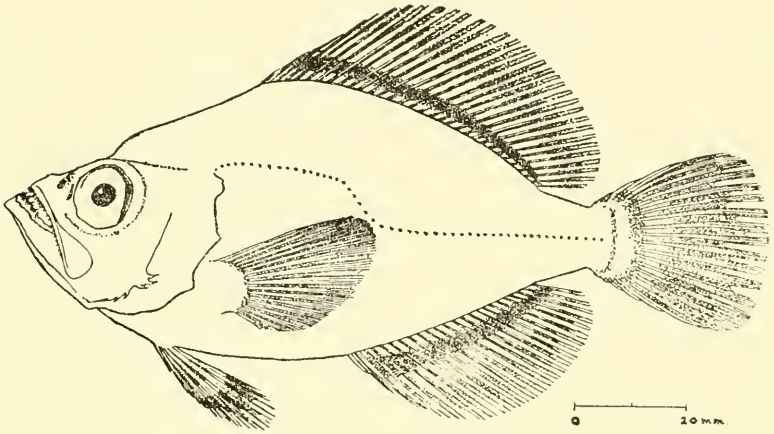


Figure 2. *Taractes* (*Taractes*) *asper*, about 110 mm. in standard length, from Madeira (from Maul, 1954:20).

which may represent the young of the third. On the other hand, Lowe's description of *T. asper* does agree well with the fishes later described from Madeira as *Trachyberyx barretoi* and from the Gulf of Mexico as *Steinegeria rubescens*. It differs from these principally in the number of scales in a lateral series (see Table 1) and in the presence of vomerine teeth. (Lunel, 1866, found the presence of vomerine teeth to be variable in some bramids, while Fowler (1936:652) suggested that they disappear with growth.) The counts of *Taractes asper* given by Lowe are com-

pared with those of our other material in Table 1. We have concluded that Lowe's *T. asper* is conspecific with Maul's Madeiran *Trachyberyx barretoi*.

### Trachyberyx barretoi Roule, 1929

The type of *Trachyberyx barretoi* was caught off Madeira and described as a new genus and species of berycoid related to *Trachichtodes*. Subsequently a series of Madeiran specimens was referred to this species by Maul and formed the basis for the account of his new and monotypic family Trachyberycidae (Maul, 1954:18). *Trachyberyx barretoi* is discussed here because Maul's specimens are not berycoids but bramids of the genus *Taractes*, closely allied to and probably identical with Lowe's "plain and sober-coloured little" type of *Taractes asper*. However, we have not definitely included the genus *Trachyberyx* Roule in the synonymy of *Taractes* or his species *barretoi* in that of *asper* because we have not been able to examine Roule's holotype, which is in the Institut Océanographique, Monaco. The general configuration of the specimen given in Roule's account is similar to that of the specimens reported by Maul (1954) and of the type of *Steinegeria rubescens*. It differs from these in fin placement, scale spines and preopercular spines. Professor d'Ancona, who examined this type for us, has forwarded information which has helped to clarify the status of Roule's species and to correct some of the errors in his description.

Professor d'Ancona has recounted the ventral fin of Roule's type and found it to be composed of a spine and five rays. Roule reported a count of I-6, the only characteristic given in the original account by which *T. barretoi* could be allied with the berycoids. On the other hand, the type has nineteen principal caudal rays (d'Ancona, personal communication), a berycoid characteristic, as opposed to the caudal count of I-15-I in Maul's Madeiran series and in all other specimens of *Taractes* which we have seen. Roule's specimen also differs in the type of spination on the scales of the caudal peduncle, for those in the midlateral series of the caudal peduncle are not notably stronger than those adjacent to them, in contrast to both Maul's specimens and the

Gulf of Mexico *T. rubescens*. Professor d'Ancona has also redescribed the preopercular spines as "approximately so arranged as in Fig. 5 of Maul's (1954) paper, not in the way represented in Roule's picture (Bull. Inst. Océan. 546)." The preopercular spines are very distinctive in our Madeiran and Gulf of Mexico juveniles. In summary, we have not been able to determine to which order or genus the type of *Trachyberyx barretoi* should be referred but suspect that it may be a species of *Taractes*.

We have dissected one of the Madeiran specimens on which the Trachyberycidae was based and have found it to differ in several important respects from the original diagnoses of the Berycoidei provided by Starks (1904:602), Regan (1911:2) and Berg (1947:467). There seems to be no orbitosphenoid, and the interorbital septum is double, at least dorsally. The supplementary maxillary is small and the maxillary is not articulated with the vomer anteriorly. The exoccipitals are separate from one another and from the basioccipital. The basioccipital is concave; the center of the concavity is slightly above the center of the vertebra. The insertion of the actinosts of the pectoral fin are equally divided between the hypercoracoid and the hypocoracoid. There are 42 (41 + 1) vertebrae. The ventral fin is composed of a spine and five branched and segmented rays. The caudal count is I-15-I. This combination of characters removes the *Trachyberyx barretoi* of Maul from the berycoids as currently understood.

We believe that the *Trachyberyx barretoi* of Maul is identical with *Taractes asper* Lowe. The adult of this form is unknown. The young, however, is closely related to the Gulf of Mexico *T. rubescens*, the adult of which is shown in the Plate. By analogy with *T. rubescens*, we expect the adult of *T. asper* to be a shallow-bodied species similar to *T. rubescens* and *T. raschi*.

### Steinegeria rubescens, Jordan and Evermann, 1887

*Steinegeria rubescens* (Figs. 3-4) was described as a new genus and species of bramid and was based on a specimen taken from the stomach of a red "grouper" caught in the Gulf of Mexico off Pensacola, Florida. This fish, in very poor condition, is now in the United States National Museum (US 37991). Subsequent to its first public description, Jordan and Evermann

(1896 :960) elevated it to family status as the Steinegeriidae, a family closely related to the Bramidae. No figure of *S. rubescens* has heretofore been published, and although the Steinegeriidae was retained as a family by Jordan and his co-authors (*e.g.* Jordan, Evermann and Clark 1930 :266), other writers, who have been unable to determine the proper position of *S. rubescens* from the description alone, have treated *Steinegeria* as a dubious genus of bramids.

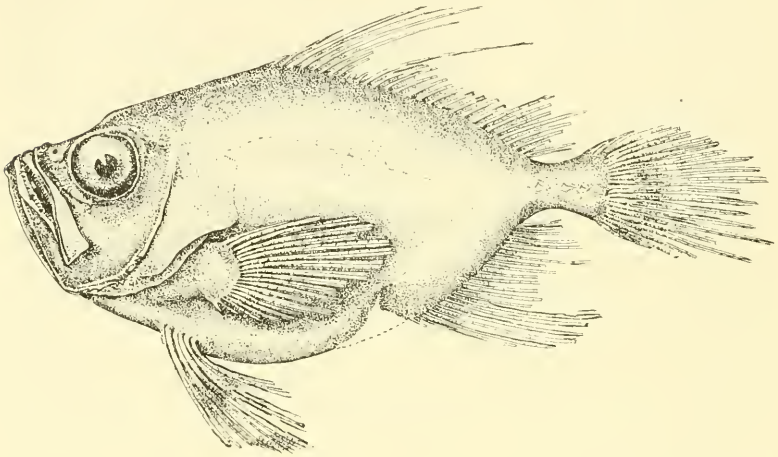

Figure 3. Holotype of *Steinegeria rubescens* (*Taractes* (*Taractes*) *rubescens*), 96.5 mm. in standard length, from the Gulf of Mexico. (Drawn by Mildred H. Carrington.)

The very poor condition of the type specimen is a handicap. The cheek bones and fins are partially digested and some elements are missing altogether. The spined scales are present, but the enlarged spines which occur on the caudal peduncle are evident on one side only. The distinctive preopercular spines which are diagnostic of the Madeiran, Gulf of Mexico, and Hawaiian juveniles are absent from one preopercular and are highly eroded on the other. The dorsal fin, said by Jordan and Evermann to be divided and thus of taxonomic merit, is composed of partially digested elements which bear indications that they were

once filamentous. Most of these elements are broken, three at their bases. (They are drawn accurately in Figure 3. Juveniles of *T. rubescens* may have a notched dorsal fin.) In addition to the several severe cuts and tears in the body wall, the fish is badly torn above the origin of the anal fin. Consequently our count of that fin as well as the measurements which include this point are of questionable accuracy. This is not a specimen from which we can draw general inferences regarding the population of which it was once a part. In spite of its condition,

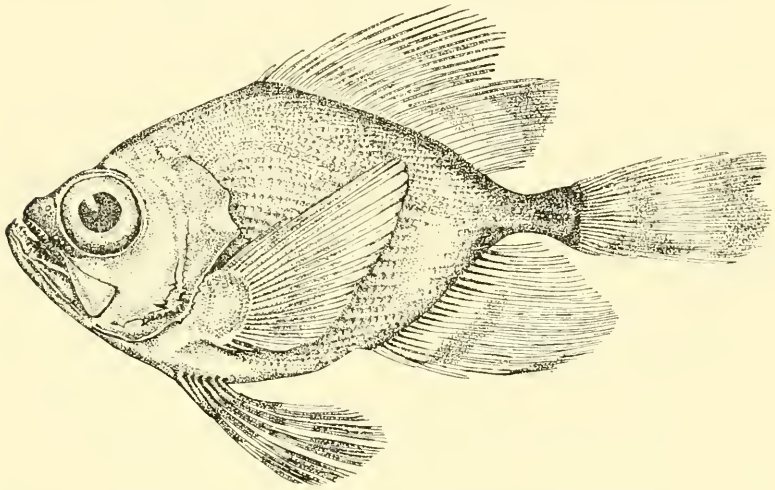

Figure 4. Juvenile *Taractes* (*Taractes*) *rubescens,* about 54 mm. in standard length, from the Gulf of Mexico. (Drawn by Mildred H. Carrington.)

however, we are convinced of its generic relationship to *Taractes.* A comparison of Figures 2 and 3 is offered in support of our view that *Steinegeria* is synonymous with *Taractes* as represented by its type species, *T. asper.*

We have referred two additional Gulf of Mexico specimens to *Taractes rubescens* — a 54 mm. juvenile and a large adult (Fig. 4, and Plate). The adult is particularly instructive, for if we are correct in considering it to be *T. rubescens,* a comparison is pos-

sible between the juvenile and the adult of this species, and between *T. rubescens* and other related species described from adult material. We believe that the caudal fin does indeed change from the rounded form which characterizes the juvenile to the emarginate type of the adult. Such a change is not out of accord with the development of the caudal fin in *T. longipinnis* (Fig. 1; Mead, 1957, Fig. 3). The development of falcate dorsal and anal fins and an increase in the number of branched rays in these fins continues beyond a fish length of 150 mm. and, as should be expected, the preopercular spines characteristic of juvenile *T.*

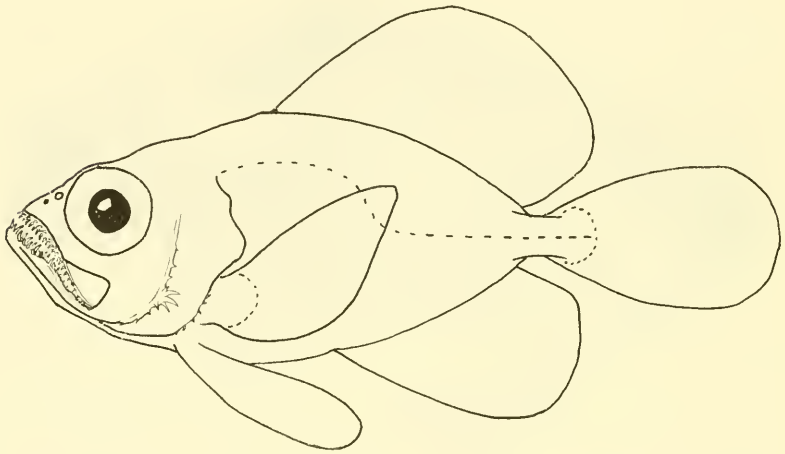

Figure 5. Juvenile *Taractes* (*Taractes*) *asper*, 56.5 mm. in standard length, from Madeira. (Drawn by Mildred H. Carrington.)

*asper* and *T. rubescens* become overgrown. It is of particular interest that another characteristic of great diagnostic value in the young, the enlarged scale spines on the caudal peduncle, is not a juvenile character but one which persists in the adult. The strong single keel which these scales form on each side of the caudal peduncle distinguishes adult *T. rubescens* from every known adult bramid specimen heretofore reported and vindicates our use of that character for the separation of the Madeiran juveniles of *T. asper* and *T. longipinnis*.

The juvenile of *T. rubescens* is quite distinct from the young Madeiran *T. asper*. The more important differences are included in our key (p. 410). The 29 mm. juvenile from off Hawaii, which is in the collection of the Pacific Oceanic Fishery Investigations, Honolulu (Fig. 6), has been compared with our 54 mm. juvenile from the Gulf of Mexico and a 30 mm. one from Madeira. It is

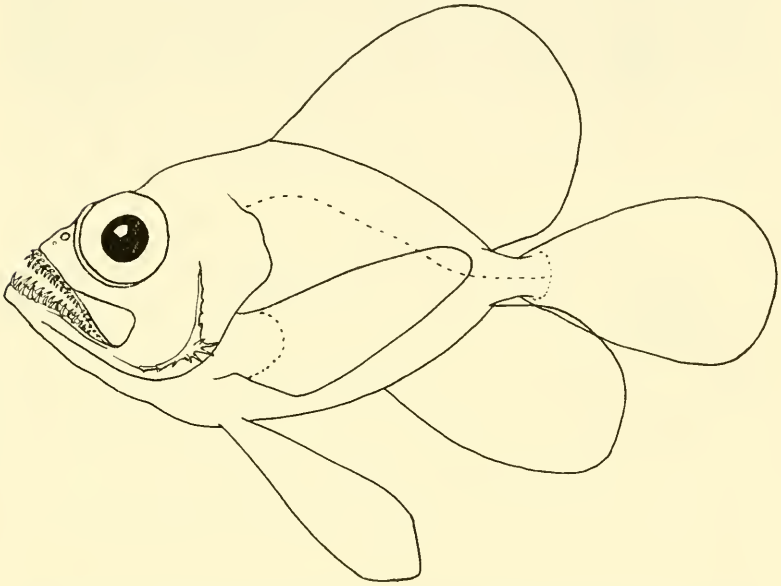

Figure 6. Juvenile *Taractes* (*Taractes*) *rubescens*, 27.5 mm. in standard length, from Hawaii. (Drawn by Mildred H. Carrington.)

similar in most respects to the Gulf specimen. Although there is reason to suspect that the Gulf of Mexico and Pacific populations are different, we are deterred from a full comparison because of the great changes known to accompany the growth of most bramid fishes, and our lack of a western Atlantic specimen of similar size. We will consider the Hawaiian juvenile conspecific with the Gulf of Mexico species until a larger Pacific specimen can be examined.

## NOMENCLATURE AND CLASSIFICATION

The recognition of *Taractes asper* as a distinct species, and of *T. asper* and the species related to it as a natural group subgenerically distinct from *T. longipinnis* and its allies, presents nomenclatorial difficulties. Most authors have applied the generic name *Taractes* to the more widely known species related to *T. longipinnis* (*longipinnis, princeps, saussuri, brevorti, steindachneri, platycephalus* and *miltonis*). We believe that *T. asper* is not a young *T. longipinnis* but a fish generically distinct from it. Unfortunately *T. asper* is the type species, and should we

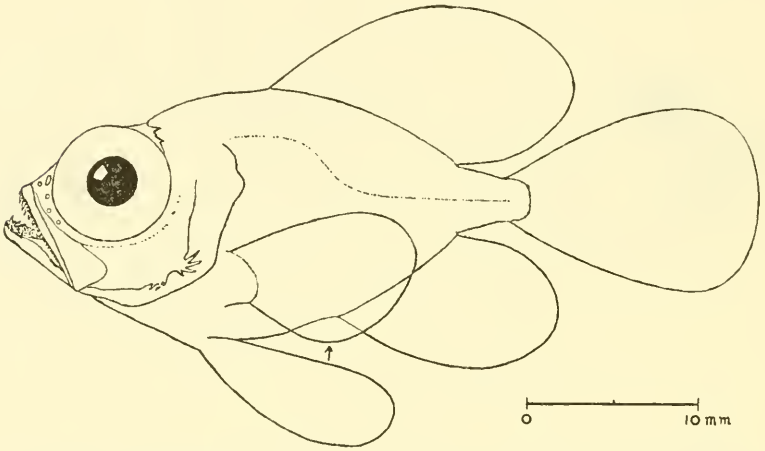


Figure 7. Juvenile *Taractes* (*Taractes*) *asper*, 30 mm. in standard length, from Madeira. (From Maul, 1954:21.)

restrict *Taractes* to its type species, *Steinegeria rubescens*, *Taractes raschi* and *T. platycephalus*, a new generic name would be needed for the commoner forms of the *longipinnis* group. We would not hesitate to propose such a change were our knowledge of Lowe's type specimen more complete or the possibility of its rediscovery more remote. We do not care to take this action without more complete information about that specimen and have consequently chosen to divide *Taractes* into two subgenera:

*Taractes*, with *T. asper* Lowe as its type species, and *Taractichthys* Mead and Maul, new, with *Brama longipinnis* Lowe as its type species. This compromise fails to recognize nomenclatorially the great differences between these two groups of species; the subgenus is used here as a nomenclatorial convenience as well as an expression of phyletic relationship. It does, however, express the close relationship between species formerly classified in widely separated groups and retains for common current use a widely-used generic name. Should our conclusions be confirmed on the rediscovery of Lowe's type, a phylogenetically more realistic classification can be established. The genera and subgenera of Bramidae (exclusive of Pteraclidae), the species of *Taractes* and the principal synonyms of each are provisionally listed below:

## BRAMIDAE

(Bramidae + Steinegeriidae Jordan and Evermann, 1896, + Trachyberycidae Maul, 1954)

### Genus Brama

*Brama* Bloch and Schneider, 1801:98. Type species (subsequent designation by Bory de St. Vincent, 1823 (3): 260): *Sparus raii* Bloch, 1791 (5):95.

Generic synonyms:

*Lepidotus* Asso y del Rio, 1801:38. Type species (monotypy): *Lepidotus catalonicus* Asso, *loc. cit.*

*Lepodus* Rafinesque, 1810:53. Type species (monotypy): *Lepodus saragus* Rafinesque, *loc. cit.*

*Tylometopon* Bleeker, 1873:133. Type species *Brama dussumieri* Cuvier and Valenciennes, 1831:294.

*Amblytoxotes* Bleeker, 1876:311. Type species (monotypy): *Toxotes squamosus* Hutton, 1875:313; 1876:210 (See Weber and de Beaufort, 1936:195).

### Genus Eumegistus

*Eumegistus* Jordan and Jordan, 1922:35. Type species (monotypy): *Eumegistus illustris* Jordan and Jordan, *loc. cit.*, p. 36.

### Genus Collybus

*Collybus* Snyder, 1904:525. Type species (monotypy): *Collybus drachme* Snyder, *loc. cit.*

## Genus Taractes

*Taractes* Lowe, 1843:82. Type species (monotypy): *Taractes asper* Lowe, *loc. cit.*

Generic synonyms:

*Argo* Döderlein, in Steindachner and Döderlein, 1883:34, pl. 7. Type species (monotypy) *Argo steindachneri* Döderlein, *loc. cit.*

*Steinegeria* Jordan and Evermann, 1887:467. Type species (monotypy): *Steinegeria rubescens* Jordan and Evermann, *loc. cit.*

Subgenus *Taractes* Lowe, 1843:82. Type species (monotypy): *Taractes asper* Lowe, *loc. cit.* (Madeira).

Species:

*Taractes* (*Taractes*) *asper* Lowe

*Taractes asper* Lowe, *loc. cit.* Günther, 1860:410 (from Lowe).

*Trachyberyx barretoi* (? non-Roule, 1929) Maul, 1954:18 (juveniles; Madeira).

*Taractes* (*Taractes*) *raschi* (Esmark)

*Brama raschi* Esmark, 1862:238 (Norway); 1868:521. Collin, 1874:418. Lilljeborg, 1884-91:310.

*Taractes raschi* Bigelow and Schroeder, 1929. Mead, 1957:56, pl. 2:4. (from Esmark), 1862, and Smitt *et al.*, 1892-95).

*Brama longipinnis* (non-Lowe). Smitt *et al.*, 1892-95:80, fig. 24 (part, after Esmark, 1862).

*Taractes longipinnis* (non-Lowe). Fowler, 1936 (2):653, fig. 293 (part?; figure stated to be after Lowe, who did not publish a figure; probably from Smitt *et al.* after Esmark).

*Taractes* (*Taractes*) *rubescens* (Jordan and Evermann)

*Steinegeria rubescens* Jordan and Evermann, 1887:467 (Gulf of Mexico)

*Taractes* (*Taractes*) *platycephalus* Matsubara

*Taractes platycephalus* Matsubara, 1936:297, fig. 1 (Japan). Mead, 1957:56 (compared with *T. raschi*).

Subgenus *Taractichthys* Mead and Maul, new. Type species: *Brama longipinnis* Lowe, 1843:82.

Species:

*Taractes* (*Taractichthys*) *longipinnis* (Lowe).

*Brama longipinnis* Lowe, 1843:82 (Madeira). Günther, 1860:410 (from Lowe, 1843).

*Taractes longipinnis.* Steindachner and Döderlein, 1884:174 (on *Argo Steindachneri* Döderlein; Japan). Barnard, 1927:595 (South African adult specimen); 1948:374

(disc. of several S. African specimens). Mead, 1957:52, pl. 1, fig. 1 (Gulf of Mexico adult and juvenile).

*Taractes asper* (non-Lowe). ?Hilgendorf, 1888:208 (specimen from the Azores said to be deposited in the Museum zu Ponta Delgada).

*Taractes princeps* Johnson, 1863:36 (Madeira). Bigelow and Schroeder, 1929 (large individual from Nova Scotia). Fitch, 1953:546 ("*Taractes* sp.," adult from California). Fowler, 1956:1 (adult from off New Jersey). Springer and Bullis, 1956:73 (several adult specimens from the Gulf of Mexico).

*Argo steindachneri* Döderlein, *in* Steindachner and Döderlein, 1883; pl. 7 (Japan).

*Taractes steindachneri* Jordan, Tanaka and Snyder, 1913:134 (Japan, listed). Matsubara, 1936:297 (compared with *T. platycephalus*).

*Taractes miltonis* Whitley, 1938:191, pl. 19 (Australia). Mead, 1957:57 (compared with Atlantic *T. longipinnis* Lowe).

*Taractes* (*Taractichthys*) *brevorti* (Poey)

*Brama brevorti* Poey, 1861 (2):206 (Cuba)

*Taractes* (*Taractichthys*) *saussuri* (Lunel)

*Brama saussuri* Lunel, 1866:185, pl. 2 (Cuba)

It must be understood that these species are among the poorest known of all fishes. Most species are known from very few specimens or from the types alone, and we have had access to few of these. The bramids are renowned for the remarkable changes in body form which take place with growth, and because of this, gross morphological characters which are of unqualified value in the taxonomic study of other groups of fishes are suspect when used in bramid classification. Among these are the presence or absence of a lateral line, shape of vertical fins, presence or absence of vomerine teeth, degree of spination on the scales of the young, and amount of branching in dorsal and anal rays. Some of these questionable characters are used, in the synopsis which follows, to distinguish between species which are known only from the type specimens (e.g. *T.* (*Taractichthys*) *saussuri cf. brevorti; T.* (*Taractes*) *platycephalus cf. raschi*), for we have not been able to examine the type material. We think that the characters used for the separation of the two subgenera and for the species of *Taractes* (*Taractes*) will prove to be valid. In any

event, the synopsis below, based as it is on very few specimens, should be considered tentative.

a. Body deep, its greatest depth less than 2.2 in standard length. Forehead high, convex and steeply inclined.
. . . . . subgenus *Taractichthys*

b. Caudal fin biconcave.

c. Central caudal fin rays extending beyond caudal lobes.
. . . . . *T.* (*Taractichthys*) *saussuri*

cc. Central caudal fin rays not extending as far as tips of caudal lobes.
. . . . . *T.* (*Taractichthys*) *brevorti*

bb. Caudal fin emarginate.
. . . . . *T.* (*Taractichthys*) *longipinnis*

aa. Body less deep, its greatest depth more than 2.2 in standard length. Dorsal profile of snout straight or concave.
. . . . . subgenus *Taractes*

d. Three or four consecutive scales of the midlateral series on the caudal peduncle enlarged and laterally produced to form, in the adult, a strong hard median keel on each side of the caudal peduncle.

e. (Juveniles) Anal fin 23 to 25, the fin originating on a vertical with the seventh to the eleventh dorsal ray. Anterior arch of the lateral line turning abruptly downward under about the eleventh dorsal ray and reaching a midlateral point below the fourteenth. The series of spines on the midlateral scales of the caudal peduncle, which are notably larger than those above and below this series, decrease gradually in length anteriorly. Least depth of caudal peduncle, in juvenile, about ten per cent of standard length. No scaleless area above and behind eye.
. . . . . *Taractes* (*Taractes*) *asper*

ee. (Juveniles) Anal fin 20 to 22, the fin originating on a vertical with the fourteenth to the nineteenth dorsal ray. Anterior arch of the lateral line curving evenly from its origin to a point on the midlateral series of scales below the twentieth dorsal ray. The series of spines on four consecutive midlateral scales of the caudal peduncle are notably and abruptly larger than those immediately anterior to them in this series as well as those immediately above and below them on the caudal peduncle. Least depth of caudal peduncle, in juvenile, about eight per cent of standard length. A scaleless area, about one-third the diameter of the eye, on body above and behind the eye and

separated from the eye by about seven rows of scales. (Western Atlantic and mid-Pacific)

..... *Taractes* (*Taractes*) *rubescens*

dd. Scales of midlateral series on caudal peduncle not enlarged; the adult without a midlateral keel on the peduncle.

f. Vomer toothed.

..... *T.* (*Taractes*) *raschi*

ff. Vomer toothless.

..... *T.* (*Taractes*) *platycephalus*

## SUMMARY

A study of a series of specimens from Madeira and the Gulf of Mexico and a comparison of this series with the nominal species of large-scaled bramids (*Taractes*) has led to the inclusion of the genus *Steinegeria* within *Taractes* and the families Steinegeriidae of Jordan and Evermann and Trachyberycidae of Maul within the Bramidae. The species of *Taractes* are divisible into shallow-bodied and deep-bodied forms, and the subgenus *Taractichthys* is proposed for the latter. *Taractes asper,* the type of which was inadequately described, subsequently lost and never illustrated, is applied to a series of Madeiran specimens formerly referred to *Trachyberyx barretoi.* Allied to this series are two juveniles and an adult from the Gulf of Mexico; these are referred to *Taractes* (*Taractes*) *rubescens,* the *Steinegeria rubescens* of Jordan and Evermann. A synopsis of *Taractes* and an enumeration of the species and principal synonyms are provided.

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| | Adult of *Taractes* (*Taractes*) *rubescens* from Gulf of Mexico | Juvenile of *Taractes* (*Taractes*) *rubescens* from Gulf of Mexico (type of *Steinegeria rubescens*) | Juvenile of *Taractes* (*Taractes*) *rubescens* from Gulf of Mexico | Juvenile of *Taractes* (*Taractes*) *rubescens* from off Hawaii | Juvenile of *Taractes* (*Taractes*) *asper* from off Madeira | Juvenile of *Taractes* (*Taractes*) *asper* from off Madeira | Type of *Trachyberyx barretoi* from Roule, 1929:4 (fig.) | Type of *Taractes asper*, from Lowe, 1843:82 |
|---|---|---|---|---|---|---|---|---|
| Standard length (mm.) | 635.0 | 96.5 | 54.0 | 27.5 | 56.5 | 113.5 | 153.0 | "Small" |
| Measurements, in per cent of standard length | | | | | | | | |
| Length of head | 30.5 | 39.4 | 41.7 | 49.4 | 40.0 | — | 33.7 | — |
| Depth of body at origin of dorsal fin | 40.1 | 50.8 | 49.1 | 54.5 | 45.3 | 48.0 | 39.5 | — |
| Least depth of caudal peduncle | 6.3 | 9.3 | 8.1 | 9.5 | 10.0 | 8.8 | 9.7 | — |
| Horizontal diam. of eye | 6.5 | 11.9 | 14.8 | 18.5 | 15.9 | 11.5 | 11.2 | — |
| Snout to origin of dorsal fin | 42.8 | 47.2 | 49.1 | 49.8 | 46.2 | 43.6 | 41.5 | — |
| Snout to origin of anal fin | 60.6 | — | 65.7 | 71.3 | 61.9 | 67.0 | 57.7 | — |
| Snout to origin of pectoral fin | 31.6 | 37.8 | 42.6 | 42.5 | 37.3 | 36.6 | 35.7 | — |
| Length of pectoral fin | 37.8 | — | 38.9 | 45.8 | 34.7 | — | 26.0 | — |
| Length of ventral fin | 12.8 | 27.5 | 33.3 | 47.6 | 36.3 | — | 22.9 | — |
| Length of longest dorsal ray | 27.4 | 26.9 | 36.1 | 44.4 | 32.7 | — | 19.4 | — |
| Length of longest anal ray | — | 24.9 | 31.5 | 44.4 | 26.5 | 24.2 | 21.3 | — |
| Length of mid-caudal ray | 9.6 | 22.3 | 31.5 | 43.6 | 34.5 | — | — | — |

| | Adult of *Taractes* (*Taractes*) *rubescens* from Gulf of Mexico | Juvenile of *Taractes* (*Taractes*) *rubescens* from Gulf of Mexico (type of *Steindachneria rubescens*) | Juvenile of *Taractes* (*Taractes*) *rubescens* from Gulf of Mexico | Juvenile of *Taractes* (*Taractes*) *rubescens* from off Hawaii | Juvenile of *Taractes* (*Taractes*) *asper* from off Madeira | Juvenile of *Taractes* (*Taractes*) *asper* from off Madeira | Type of *Trachyberyx barretoi* from Roule, 1929:4 (fig.) | Type of *Taractes asper*, from Lowe, 1843:82 |
|---|---|---|---|---|---|---|---|---|
| Counts: | | | | | | | | |
| Dorsal fin | 31 | 29½ | 30½ | 31½ | 32½ | 32 | 32 | 33 |
| Anal fin | 20½ | 21½ | 21½ | 21 | 23½ | 25 | 25 | 23 |
| Pectoral fin | 20 | 21 | 20 | 21 | 18 | — | 20 | 17 |
| Ventral fin | I-5 | I-5 | I-5 | I-5 | I-5 | I-5 | I-5 | I-5 |
| Caudal fin | I-15-I | I-15-I | I-15-I | I-15-I | I-15-I | I-15-I | "19" | 4 + VIII<br>3 + VII |
| Gill rakers | 2+8 | 2+8 | 2+9 | 2+7 | 2+7 | 2+7 | — | — |
| Scales in median longitudinal series | 49 | — | 52 | 48 | 49 | — | 49 | 43[3] |
| Vertebrae (incl. hypural) | 42 | 42 | — | — | — | 42 | — | — |

TABLE 1 — Proportional measurements and counts taken from an adult and three juvenile specimens of *Taractes* (*Taractes*) *rubescens* from the Gulf of Mexico and off Hawaii, two juveniles of *Taractes* (*Taractes*) *asper* from off Madeira, the type specimen of *Trachyberyx barretoi* (from Roule) and that of *Taractes asper* (from Lowe)

[3] If Lowe excluded from his count the scales on the caudal peduncle which merge to form a keel, his enumeration of the scales in a longitudinal series is in accord with our counts of other juvenile Madeiran specimens.

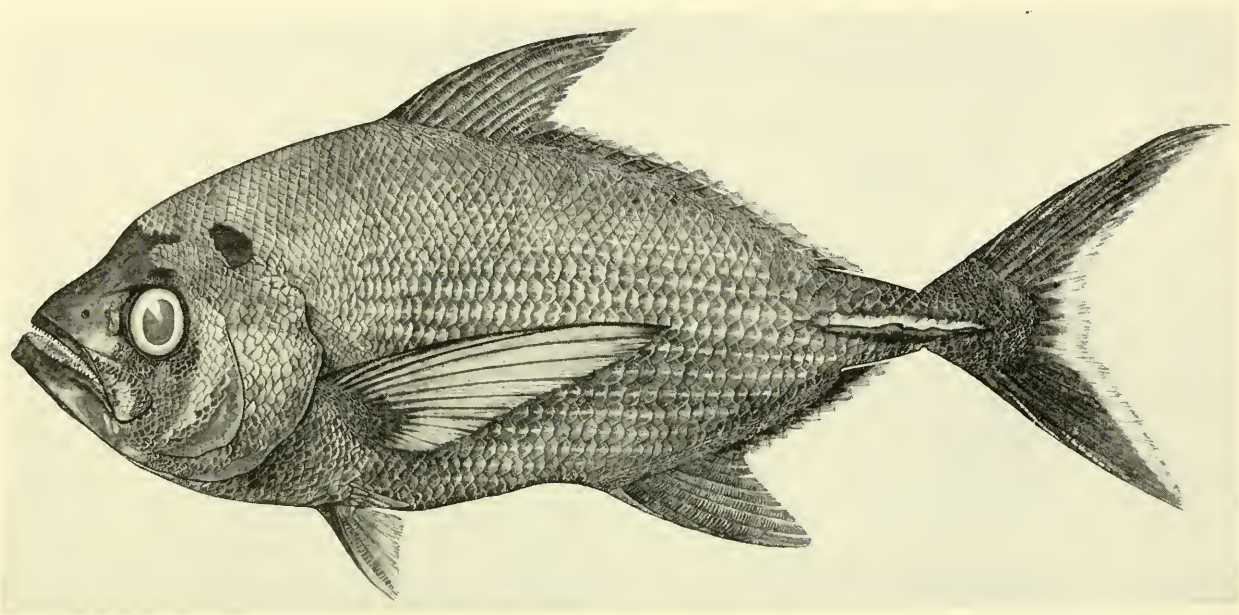

Plate. Adult *Taractes* (*Taractes*) *rubescens*, 635 mm. in standard length, from the Gulf of Mexico. (Drawn by Mildred H. Carrington.)

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# ADDITIONS TO THE PLEISTOCENE MAMMALIAN FAUNA FROM MELBOURNE, FLORIDA

By Clayton E. Ray

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
November, 1958

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*No. 7 — Additions to the Pleistocene Mammalian Fauna from Melbourne, Florida*

By Clayton E. Ray

## INTRODUCTION

Of the 33 genera of native wild mammals (exclusive of bats, whales, and seals) now or recently living in Florida, 31 have been recorded from the Pleistocene. The two genera not yet reported are small forms (*Sorex* and *Glaucomys*) which might easily escape notice and which for obvious reasons must be rare fossils in any case. In addition to the 31 genera known both from the Pleistocene and from the Recent, 25 are known from the Pleistocene only, of which 14 have subsequently become totally and 11 locally extinct. The discovery of fossil human remains at Vero (Sellards, 1916) and at Melbourne (Loomis, 1924) has lent great impetus to the study of the Pleistocene in Florida, and is thus in part responsible for our relatively complete knowledge of the mammalian fauna. A large fraction of the literature on Floridian vertebrate paleontology is devoted to the interpretation of these controversial human remains, with which problem the present communication is not directly concerned.

Published information regarding the fossil mammals (exclusive of man) of Melbourne is in no way commensurate with the potentialities of the extensive museum collections from the locality, a situation due primarily to the untimely death of Dr. J. W. Gidley of the U. S. National Museum who supervised field work at Melbourne during the 1920's and who intended to report upon the mammals. Most of the 84 papers listed by Ray (1957) deal with human remains or with vertebrates other than mammals. Particularly neglected in the literature is a large series of fossils from Melbourne in the Museum of Comparative Zoology, known as the Singleton Collection. The only studies of the mammals in this collection are the description of *Molossides floridanus* by Allen (1932), the discussion of a jaw of *Dasypus bellus* by Simpson (1929B, p. 577), and the discussion of $P^3$ of *Tanupolama mirifica* by Bader (1957, p. 61). That the existence of the Singleton Collection is generally unknown is indicated by Rouse's ignorance of it in his very careful studies (1951, p. 154), and by the

recorded "disappearance" of certain specimens which are in fact in the Singleton Collection (see under *Homo sapiens* and *Dasypus bellus* below).

It seems useful to outline the history of the collection in order to supplement the inadequate field data and thereby to establish as clearly as possible the locality and horizon of the specimens. The Singleton Collection was acquired in 1928 through the efforts of Dr. Thomas Barbour, then Director of the Museum, who states (1929, p. 6) as follows: "In cooperation with the United States National Museum, Mr. C. P. Singleton continued to excavate in the Pleistocene deposits near Melbourne, Florida, during the months when he was not employed by Dr. Gidley. Dr. Gidley is preparing a report on this material. The described specimens then will be forwarded to Cambridge — that is those which were obtained by Mr. Singleton during the half year in which he was working for us." The projected report was never published, due to Gidley's death in 1931 shortly after his last season at Melbourne. As anticipated by Barbour, that portion of the collection belonging to the Museum of Comparative Zoology was indeed forwarded to Cambridge where it has remained unstudied and in part uncatalogued to the present time. The chance discovery of the jaw of a wolf-like canid among this material suggested that other new information might be gleaned from this long-dormant source, and the entire Singleton Collection was accordingly examined. As might be expected, most of the species are represented by comparable or better material in the U. S. National Museum. A cursory examination of the Amherst College collection has revealed nothing to be added to the report by Loomis (1924, p. 506). The Singleton Collection yields seven species new to the Melbourne locality (*Blarina brevicauda*, *Peromyscus gossypinus*, *Synaptomys australis*, *Mephitis mephitis*, *Felis* cf. *inexpectata*, *Canis* cf. *lupus*, and *Monachus tropicalis*) of which two (*Canis* cf. *lupus* and *Monachus tropicalis*) are new to the recorded Pleistocene fauna of Florida, and one (*Monachus tropicalis*) is here recorded as a fossil for the first time.

## STRATIGRAPHY

Some uncertainty exists regarding the provenance of individual specimens from the Singleton Collection. Pleistocene fossils

have been collected from two major localities in the vicinity of Melbourne,[1] both discovered by Singleton. The first of these, reported to the National Museum in 1922, is 1.5 miles southwest of Melbourne and has been called the Singleton Estate locality. Loomis excavated here during December, 1923, obtaining a small but representative fauna (Loomis, 1924). Since little if any work was carried on at this site during subsequent years, and since Singleton divided his collections as of 1925 between Amherst College and the U. S. National Museum (Gidley and Loomis, 1926, p. 255), it appears improbable that any material from the Singleton Estate locality became incorporated into the Singleton Collection. Beginning in 1925, with a joint project between Amherst and the National Museum, and continued in later years (through 1930) by the National Museum alone, excavations were concentrated at the "Golf Course" locality, Melbourne. Singleton was employed during the field seasons of all these years, and it was at the Golf Course locality that he and Gidley collected during the winter of 1928-29. Recalling Barbour's statement that Singleton continued field work for the Museum of Comparative Zoology during the months immediately following, the Golf Course locality seems to be the most probable source of the Singleton Collection. The museum labels record the locality simply as "Melbourne," with the exception of those accompanying the specimens of *Peromyscus gossypinus* and *Canis* cf. *lupus* which read "Melbourne, 2 miles west of." It was at first suspected that these labels indicated some locality other than the Golf Course and that the fossils might therefore not necessarily be derived from beds of certain Pleistocene age (Stratum 2). However, in response to the present author's query, Dr. C. L. Gazin of the National Museum has very kindly supplied (*in litt.*, October 29, 1956) the following information: "With regard to the location 'Melbourne 2 mile W,' this must mean the golf course, as I note on several labels here in Gidley's handwriting the statement 'Golf links, 2 miles west of Melbourne.'" Thus it seems safe to assume that the Singleton Collection derives from the Golf Course locality.

[1] A comprehensive account of the history of discovery, the geography, and development of the Melbourne finds is that of Gidley and Loomis (1926).

The Quaternary stratigraphy at the Golf Course locality is summarized in Table 1. At the time of discovery of human remains at Vero, Sellards (1916) considered both Stratum 2 and Stratum 3 to be Pleistocene in age. Owing to the widespread interest in human paleontology, the age of these beds and of the included fossils has been heatedly debated during the intervening 40 years, resulting in the accumulation of a voluminous polemic literature. Rouse (1951, pp. 30-34, 153-162, 234-237) may be consulted for a useful nonpartisan review of the evidence.

In brief, the evidence indicates that Stratum 2, containing abundant, primarily deposited extinct mammals, is late Pleistocene in age. Stratum 3 is Recent[2] in age, the supposedly extinct species in it having been synonymized with living species, or considered to be redeposited. The human remains were deposited in the upper layers of Stratum 2 or on the erosion surface above Stratum 2 (Rouse, 1951, p. 157).[3]

In regard to the source bed of the fossils of the Singleton Collection, it seems almost certain that all are derived from Stratum 2. Although this is not explicitly stated on the museum labels, all specimens are labeled "Pleistocene." Such an assertion would scarcely have been made for fossils collected in Stratum 3 in view of its controversial age. In particular, Singleton who had long collecting experience both in Florida and in the western states, and who had worked with Gidley at Melbourne during the months immediately prior to collecting for the Museum of Comparative Zoology (as well as during preceding years), must have been aware of the extreme importance of segregating collections from the two strata. Furthermore, as indicated by Barbour, the Singleton collection and the National Museum collections were to be studied as a unit by Gidley, who certainly would not have mingled fossils from the two strata. Simpson (1929B, p. 579) implicitly considered the jaw of *Dasypus bellus* (described by him and discussed in the present report) to be derived from Stratum 2. The jaw of *Panthera augusta* from Melbourne described by Simpson (1941, p. 6) "is not exactly

[2] Following Morrison *et al.* (1957, p. 387) who quote with approval a statement by Lyell that "in the Recent we comprehend those deposits in which not only the shells but all the fossil Mammalia are of living species."

[3] On the basis of fluorine tests, Heizer and Cook (1952, p. 299) found samples of mammoth, horse, and human bone from Melbourne to be of a similar order of antiquity. The reliability of the fluorine evidence remains to be established.

TABLE 1

| FORMATION | AGE | THICKNESS IN FEET | LITHOLOGY (from Cooke and Mossom, 1929, p. 219). |
|---|---|---|---|
| Van Valkenburg Beds (Sellards, 1940, p. 383), Stratum 3 (Sellards, 1916). | Recent | 0-5 (Cooke and Mossom, 1929, p. 219); 1.5-2 (Gidley and Loomis, 1926, p. 258); 3-4 (avge.) (Gidley, 1929, p. 15). | "Swamp and stream deposits consisting of peat and partly decomposed roots, bark, and leaves, interstratified with yellowish or drab sand containing fresh-water mussel shells." |
| Melbourne Bone Bed (Cooke and Mossom, 1929, p. 218), Stratum 2 (Sellards, 1916). | Pleistocene | 1-10 (Cooke and Mossom, 1929, p. 219). | "Fine white to light-brown sand containing a few local irregular lenses of marine shells and local accumulations of bones; where shell lenses are absent this bed appears massive or is streaked horizontally by dark carbonaceous sand." |
| Anastasia Formation (Sellards, 1912, pp. 7, 18), Stratum 1 (Sellards, 1916). | Pleistocene | Base not exposed. | "Coarse sandy coquina composed of rather firmly cemented broken shells and sand; base not exposed." |

TABLE 1. Quaternary stratigraphy at the Golf Course locality, Melbourne, Florida.

labeled as to horizon but doubtless came from the 'No. 2 bed' or Melbourne formation." Gazin (1950, p. 397) found the National Museum collections to be inadequately labeled, but was convinced that their source was in or at the top of Stratum 2.

Thus, in spite of the lack of adequate data accompanying fossils of the Singleton Collection, the present author considers as established their derivation from Stratum 2 at the Golf Course locality, Melbourne.

## FAUNA[4]

### Marsupialia

*Didelphis marsupialis* Linnaeus 1758, M.C.Z. 17767, 17768, 17770-17773.

An opossum indistinguishable from the modern North American species is represented by a considerable number of bones, including six more or less complete mandibular rami, three maxillae, 10 limb bones, some two dozen vertebrae, and about 20 fragments of skulls and jaws.

### Insectivora

*Blarina brevicauda* (Say) 1823, M.C.Z. 17793.

The short-tailed shrew, hitherto unknown from Melbourne and reported elsewhere in the Pleistocene of Florida only from Vero and Arredondo, is represented by two right mandibular rami, one of them essentially complete but having lost all teeth except $I_3$, the other lacking the anterior end but retaining well-preserved $M_1$-$M_3$. Both jaws are slightly smaller than available comparative specimens, but otherwise are quite characteristic of the species.

*Scalopus aquaticus* (Linnaeus) 1758, M.C.Z. 17792.

Three mandibular rami, four ulnae, and 14 of the highly characteristic humeri are included.

[4]The author wishes to point out that most of the specimens in the Singleton Collection bore museum identifications which upon checking proved to be generally well founded. These identifications are probably to be credited to Drs. J. W. Gidley and G. M. Allen. Throughout the discussion, M.C.Z. stands for Museum of Comparative Zoology, C.N.H.M. for Chicago Natural History Museum, U.S.N.M. for United States National Museum, and A.M.N.H. for American Museum of Natural History.

## Chiroptera

*Molossides floridanus* G. M. Allen 1932, M.C.Z. 17672.

This monotypic genus is known only from the type specimen, a left mandibular ramus with well-preserved $M_1$-$M_3$. Allen (1932) may be consulted for description and illustration of the jaw.[5]

## Primates

*Homo sapiens* Linnaeus 1758, M.C.Z. 5909, 5910, 17839, 17840. Harvard Peabody Museum A6289, A6296, A7442-A7452, A9611, A9612, 35619-35622.

The Singleton Collection contains no human bones, but several artifacts attest to the presence of man. The artifacts, excepting four mammal bones, have been transferred to the Peabody Museum. The mammal bones are three carved and polished mandibular rami of *Odocoileus virginianus* and a carved partial left maxilla and premaxilla with the canine tooth preserved of *Canis* sp. Most interesting of the artifacts is a crude stone blade found on exhibition in the Museum of Comparative Zoology. This specimen bears U. S. N. M. No. 342,218 and a gummed label reading as follows: "Found directly under and in contact with mastodon bone. *Harvard* C.P.S. 1928." Apparently Singleton's label was noticed after the specimen had been inadvertently catalogued in the National Museum whereupon it was sent on to Cambridge where it remained unnoticed, on exhibition, until rediscovered in 1957 and catalogued by the Harvard Peabody Museum (35619). This history explains Rouse's inability to find the specimen in the National Museum (1951, p. 158). The specimen is apparently that referred to by Gidley and Singleton (1929, p. xiv), as suspected by Rouse. It has been referred to also by Gidley (1931, p. 41) who considered it to represent "additional evidence of early man in Florida." Stephen Williams of the Peabody Museum contemplates a more detailed report on this and the other artifacts from Melbourne.

[5] This specimen is housed in the collection of types in the mammal department. All others, excepting most artifacts which are in the Peabody Museum, are in the vertebrate paleontological collection. All M.C.Z. numbers are those of the Department of Vertebrate Paleontology.

## Edentata

*Megalonyx* cf. *wheatleyi* Cope 1871, M.C.Z. 17774, 17775.

*Megalonyx* is represented in the Singleton Collection by 10 tooth fragments, a right humerus and a right femur. The limb bones are without epiphyses and are spongy in texture, indicative of youth. These bones together with the teeth are here tentatively referred to *M. wheatleyi* following the examples of Simpson (1928, pp. 11-13) and of Gazin (1950, p. 398). This reference constitutes little more than a nomenclatural convenience pending a revision of the genus.

*Paramylodon* cf. *harlani* (Owen) 1840, M.C.Z. 2967.

A well preserved supraoccipital bone furnishes the basis for recording *Paramylodon* in the Singleton Collection. The bone, apparently that of a young individual, shows the characteristic development of sinuses between the dorsal internal and external tables of the skull. The inner table reveals a well-preserved cast of the cerebellar surface.

*Dasypus bellus* (Simpson) 1929, M.C.Z. 17802, 17803, fig. 3.

This species is represented by the distal half of a right humerus, a right radius, a right third metatarsal, a left calcaneum, a phalanx, three isolated teeth, several hundred dermal scutes, and a single fragment of a left lower jaw with four teeth in place and an alveolus for a fifth tooth anterior to these, and by a single isolated tooth accompanying the jaw. The jaw corresponds in every respect to that described by Simpson (1929b, p. 579) in his original description of the species:[6] "Through the courtesy of Dr. Gidley I have been able to examine a jaw of this species, collected by C. P. Singleton at Melbourne, and hence to identify other isolated teeth. The Melbourne specimen includes five teeth and an alveolus for another anterior to these. There was probably one and perhaps several more teeth in the complete jaw. The more anterior teeth are elongate, with flattened sides and rounded ends, wider posteriorly than anteriorly. The more posterior teeth are nearly circular, the largest slightly wider than long. They reach a maximum length of about 5 mm., depth about 13 mm."

[6] This fact was recognized by G. M. Allen, as indicated by a note in his handwriting accompanying the specimen.

The fifth and hindmost tooth has obviously become detached since Simpson's description, but remains with the jaw, and has been replaced for purposes of illustration. As stated by Simpson, Gidley was quite naturally in possession of the specimen in 1929, but that it belongs to the Singleton Collection and is, in fact, the jaw discussed here, is verified by Gazin's (1950, p. 399) failure to find it in the National Museum collections. The species has been reported from eight additional localities in Florida and from a cave in St. Louis, Missouri (Simpson, 1949, p. 11), but so far as the literature reveals, the present specimen is the only dentigerous element known.

*Chlamytherium septentrionalis* (Leidy) 1890, M.C.Z. 17794, 17795.

Material referable to this extinct giant armadillo-like edentate includes more than 100 dermal scutes (17795) and six teeth (17794). James (1957) is followed in synonymizing *Holmesina* Simpson 1930 with *Chlamytherium* Lund 1838.

## Lagomorpha

*Sylvilagus palustris* (Bachman) 1837, M.C.Z. 17776, 17777.

Some 24 fragmentary mandibular rami, three fragmentary upper jaws, and miscellaneous limb bones are referred to the marsh rabbit. All material was examined with especial attention to the possibility of the pygmy species, *Sylvilagus palustrellus*, being represented in the collection. This species was described by Gazin (1950, p. 399) on the basis of a left mandibular ramus from Melbourne (type) and a second, possibly sub-Recent, specimen from Sugarloaf Key.[7] Species characteristics are given as follows: size ⅔ that of *S. palustris*, jaw shallow, teeth relatively narrow transversely, and anterior wall of $P_3$ with a single shallow fold. None of the specimens at hand seems to fulfill these requirements. Of the 13 rami with $P_3$ in place, all show at least two crenulations on the anterior wall of $P_3$. Two of these rami are small in size but retain the $P_3$ typical of *S. palustris* and can be matched almost perfectly in size, propor-

[7] In this connection, it may be noted that one Colonel Patterson of Key West, Florida, informed De Pourtales (1877, p. 142) of the possibility that the "aquatic rabbit" ranged as far as Key West and that "a burrowing rabbit" is found on Rabbit Key (N.25°, W.80°50'). Neither Nelson (1909), Hall (1951), nor Schwartz (1956) record rabbits from the Keys.

tions, and texture ("sponginess") by immature Recent *S. palustris* (as M.C.Z. 3420).

*Sylvilagus palustrellus* should be compared to *Sylvilagus leonensis* (also a pygmy) described by Cushing (1945, p. 183) from San Josecito Cave, Nuevo Leon, Mexico. Unfortunately neither description is accompanied by illustrations. *Sylvilagus palustrellus* may be related to the lagomorph from Vero which Sellards (1916, p. 15) compared to *Romerolagus* and *Pronolagus* but considered to represent a new genus (which he never described). It seems that the Pleistocene lagomorphs of Florida might profitably be re-examined.

## Rodentia

*Geomys pinetis* Rafinesque 1817, M.C.Z. 17779, 17780.

The pocket gopher is represented by some 70 mandibular rami (mostly fragmentary), a palate with $P^4$ and $M^1$ on both sides, a rostrum with one incisor, nine isolated upper incisors, and miscellaneous limb bones. The fossils are indistinguishable from the species presently living in the area. No remains of *Plesiothomomys* were discovered in the collection.

*Oryzomys palustris* (Harlan) 1837, M.C.Z. 17786, Fig. 1B.

The rice rat is represented by eight mandibular rami, only one of which is considered to be strictly identifiable to species. With the exception of this single relatively complete specimen in which $M_1$ and $M_2$ are preserved, the jaws are without cheek teeth. Previous records of the rice rat from Melbourne are generic only. In addition to *Oryzomys palustris* the fossil specimens were compared with *O. couesi*, *O. rostratus*, *O. alfaroi*, *O. talamancae*, and *O. devius*, and were found to be readily distinguishable from all of them except *O. palustris*. Of the forms examined, *O. couesi* seems to approach *O. palustris* most closely.

The differing configuration of the insertion scars of *M. masseter medialis, pars anterior* and of *M. masseter lateralis profundus, pars anterior* (see Rinker, 1954, p. 16, fig. 1B) on the lateral surface of the mandibular ramus seems to be a character useful in distinguishing certain closely related species of cricetine rodents. If substantiated by examination of more specimens than have been available to the author, such a character would be of value in the identification of toothless jaws. *Oryzomys*

*palustris* is distinguished from *O. couesi* on the basis of the sharp dorsad flexure of the anterior portions of the two masseteric scars in the latter species. As seen in labial view with the toothline taken as the horizontal (Fig. 1B), the more dorsal of the

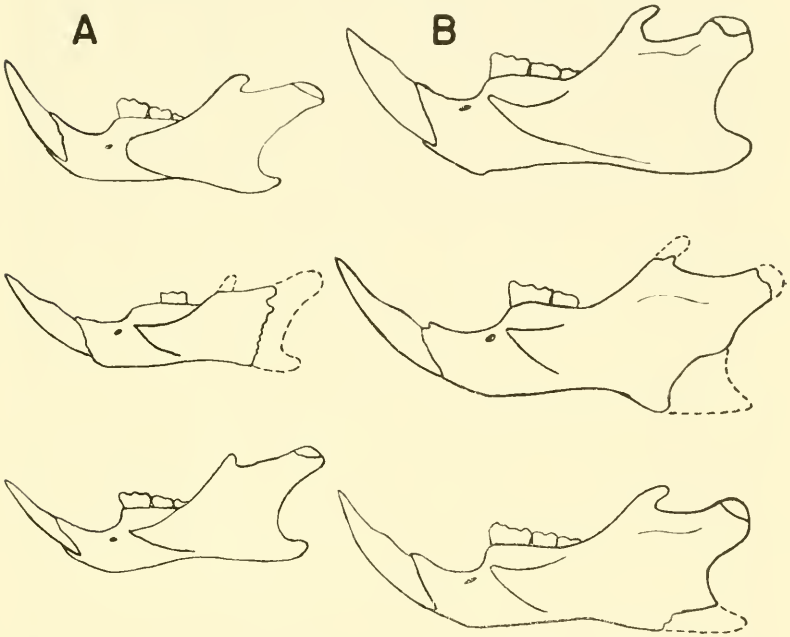


Figure 1*A*. Labial view of left mandibular rami of *Peromyscus nuttalli* (M.C.Z. 1491, top), *P. gossypinus*, fossil (M.C.Z. 17778, center), and *P. gossypinus* (M.C.Z. 3226, bottom). X2.75.

1*B*. Labial view of left mandibular rami of *Oryzomys couesi* (M.C.Z. 1532, top), *O. palustris*, fossil (M.C.Z. 17786, center), and *O. palustris* (M.C.Z. 4465, bottom). X2.75.

two scars (*M. masseter medialis*) in *O. couesi* is deeply concave upward having its most ventrad extension under the point between $M_1$ and $M_2$. In contrast, the most ventrad point on the scar in *O. palustris* lies at or near the apex of the V formed by

the anterior intersection of the two masseteric scars. The jaws from Melbourne resemble *O. palustris* in configuration of the masseteric scars.

*Peromyscus gossypinus* (Le Conte) 1853, M.C.Z. 17778, Fig. 1A.

The cotton mouse is represented by two left mandibular rami, both of which retain incisors but lack cheek teeth with the exception of a very worn $M_2$ in one of the specimens. Records of the genus in the Pleistocene of Florida are highly unsatisfactory and certainly not indicative of true rarity. Gut (1939, p. 55) reports *Peromyscus* sp. from Reddick, Marion County; Bader (1957, p. 54), *Peromyscus* sp. from Arredondo; Sherman (1952, p. 92-93), *P. gossypinus* and *P. floridanus* without locality data.[8]

The specimens were compared with series of *P. floridanus*, *P. polionotus*, *P. nuttalli*, and *P. gossypinus*. Gross size readily distinguishes the fossils from *P. floridanus* and *P. polionotus*, the former being larger and the latter smaller than the fossils. Recent specimens of both *P. nuttalli* and *P. gossypinus* correspond in size to the fossils. As in the case of *Oryzomys* (above), the two species in question can be distinguished on the basis of the configuration of the scars of *M. masseter medialis, pars anterior*, and *M. masseter lateralis profundus, pars anterior*. In *P. gossypinus* the anterior portions of the scars intersect in a narrow, sharply-pointed V, the apex of which is directed dorsad with the *M. masseter medialis* scar consequently concave upward as seen in lateral view (Fig. 1A). The same scars in *P. nuttalli* intersect anteriorly in a broadly rounded U, the apex of which is directed ventrad with the *M. masseter medialis* scar more nearly straight and more steeply inclined relative to the tooth row than in *P. gossypinus*. In series of approximately 30 jaws of each species, the configurations described were found to be somewhat variable, but in all cases distinguished the species. The fossil jaws are typical of *P. gossypinus* in regard to the masseteric scars.

*Sigmodon hispidus* Say and Ord 1825, M.C.Z. 17798.

Some 64 lower jaws, many with complete dentition, three maxillary fragments, and about 25 limb bones of the cotton rat are present in the collection.

[8] Sherman *(in litt.,* November 18, 1956) states that these records are from the Reddick locality and that they are based on personal communications from Mr. Gut. At Dr. Sherman's request, this opportunity is taken to credit the first report of the species *Peromyscus gossypinus* and *P. floridanus* in the Pleistocene of Florida to Mr. Gut.

*Neotoma floridana* (Ord) 1818, M.C.Z. 17799.

The wood rat is represented by 30 mandibular rami and a fragmentary maxilla with $M^1$.

*Synaptomys australis* Simpson 1928, M.C.Z. 17785.

The southern bog lemming, hitherto known only from the type locality of Saber-tooth Cave and from Arredondo, can now be recorded from Melbourne on the basis of four fragmentary rami of lower jaws, all of which are somewhat smaller than the type specimen (Simpson, 1928, p. 7). The triturating surface of the molars in the only specimen with complete dentition is 8.0 mm. in length as compared to 8.4 mm. in the type. One of the rami (without molars) is quite comparable to the living *S. cooperi* in size, but apparently is a young *S. australis,* being distinguished from *S. cooperi* by the more open arc described by its incisor. Indistinct, rounded muscle scars and crests are suggestive of youth in the specimen.

*Neofiber alleni* True 1884, M.C.Z. 17796, 17797.

The round-tailed muskrat is represented by the following specimens: 34 mandibular rami, three palatal fragments, numerous isolated molariform teeth, and 16 posteranial elements. The absence of *Ondatra* from the collection adds further weight to the contention of Neill (1957, pp. 7, 8) that the two genera were allopatric during the Pleistocene just as they are at present.

## Carnivora

*Aenocyon* sp., cf. *A. ayersi* (Sellards) 1916, M.C.Z. 5912.

Remains of *Aenocyon* consist of the distal one third of a left humerus, a left radius lacking the proximal extremity, a cervical vertebra, and a distal fragment of a metapodial.

*Canis* sp., cf. *C. latrans* Say 1823, M.C.Z. 5909, 17790.

A coyote-sized canid is represented by two calcanea, an astragalus, and a rostral fragment consisting of the left premaxilla and the adjacent portion of the left maxilla with $C^1$. The bones are indistinguishable from the living *Canis latrans.* The species *C. rivivcronis* Hay 1917, described from Stratum 3 at Vero, is inadequately separated from *C. latrans.* In his original diagnosis Hay (1917, pp. 59, 60) noted overlap with *latrans* in each of the supposedly distinguishing characters. There is in Hay's description no basis upon which *rivivcronis* can be distinguished from *latrans* and it is here placed in the synonymy of the living species.

The tooth-bearing fragment (M.C.Z. 5909) is an artifact. Its dorsal border is a straight, polished edge paralleling the palatal surface at the level of the root-tip of the canine. Its posterior border is a straight edge perpendicular to the dorsal border and bisecting the posterior root of $P^2$.

*Canis* sp., cf. *C. lupus* Linnaeus 1758, M.C.Z. 17789, Fig. 2.

Although *Aenocyon* is known from at least eight localities including Melbourne, the present record is the first for a wolf of modern type from the Pleistocene of Florida. Simpson

Figure 2. Labial view of left mandibular ramus of *Canis* sp., cf. *C. lupus*, M.C.Z. 17789. X 2/3.

(1929b, pp. 572-573) notes a larger and a smaller size class within the large canid material from Saber-tooth Cave and Seminole Field but tentatively refers both groups to *Aenocyon ayersi*. The smaller form falls within the size range of modern *C. lupus*, however, and may very well pertain to that species.

The present record is based upon a well-preserved left mandibular ramus[9] lacking angular and coronoid processes and the anterior extremity beyond the canine alveolus but with $P_2 - M_2$ present and undamaged (excepting the postero-lateral corner of $M_1$). In spite of the relative completeness of the jaw, it was not possible to definitely establish its specific identity.[10] According to the most recent comprehensive review (Goldman, 1944) there are two living species of North American wolves, *C. lupus* and *C. niger*, the latter being distinguished by its

[9]The specimen is accompanied by a field label indicating that it was collected from a depth of four feet which would seemingly place it within Stratum 2. The label is dated June 23 (presumably 1929) and initialed by C. P. Singleton.

[10]The field label bears the note initialed by Gidley, "compare *Canis lycaon*," now *Canis lupus lycaon*.

smaller size, more slender skull, more deeply cleft molariform teeth, more laterally compressed cusps of molariform teeth, and more trenchant points and shearing edges of molariform teeth (Goldman, pp. 478-481). Both species have been at least tentatively identified from Florida, *C. niger niger*[11] having been originally described from Florida and *C. lupus* recorded on the basis of a skull (M.C.Z. 11179) from somewhere in Florida (Goldman, p. 440). Examination and measurement of the eight jaws of *niger* in the Museum of Comparative Zoology and the American Museum of Natural History and of a great many jaws of *lupus* led to the conclusion that the species are sufficiently similar in size as to be indistinguishable (on the basis of lower jaws) unless sex and age are known and taken into consideration, and perhaps not then (Table 2). The characters of the cheek teeth were considered to be inadequate for a reliable conclusion to be made

*Vulpes* sp., cf. *V. palmaria* Hay 1917, M.C.Z. 5857.

The genus *Vulpes* is represented by the distal half of a right humerus and by a left second metatarsal. These bones compare closely with those of modern *V. fulva*. At the time of Hay's description (1917, p. 57) of *Vulpes palmaria* from Stratum 3 at Vero, the living North American red foxes were distributed taxonomically among at least ten "species," whereas they are now assigned to one, with former species names reduced to subspecies. Hay compared and contrasted the fossil primarily with *V. fulva fulva*, one of the smaller subspecies as now understood. Examination of the very large series of *V. fulva* in the Museum of Comparative Zoology revealed none with a lower jaw quite so deep as that of the type specimen of *V. palmaria*. Only the largest modern jaw (M.C.Z. 34097) approaches the fossil closely in this regard (Table 3). In view of this slight size discrepancy and of the remote possibility that some or all of modern North American red foxes are descendants of introduced European stock (Palmer, 1956, pp. 67, 68), it seems best to retain the name *palmaria* until better Pleistocene material is found. Further discoveries may indicate that *palmaria* is a robust Pleistocene subspecies of *V. fulva*.

[11] Unfortunately only two skulls of the type subspecies found their way into museum collections before the animal became extinct. A third skull (M.C.Z. 11179) tentatively assigned to *C. lupus lycaon* may pertain to *C. niger*.

| | *Canis* (?) *lupus*, M.C.Z. 17789, Melbourne, Florida, Pleistocene. | *Canis* (?) *lupus*, M.C.Z. 11179, Florida. | *Canis niger gregoryi*, M.C.Z. 21531, Poplar Bluff, Missouri, male. | *Canis lupus nubilus*, M.C.Z. 65, northwestern Kansas. | *Canis lupus lycaon*, M.C.Z. 40936, Wisconsin. | *Canis lupus pallipes*, C.N.H.M. 44468, Seri Hassan Beg. Mmts., Iraq. |
|---|---|---|---|---|---|---|
| Length of $P_2$ | 11.3 | 11.9 | 11.5* | 6.9 | 12.5 | 12.2 |
| Width of $P_2$ | 5.3 | 5.8 | 5.4 | 2.8 | 6.4 | 6.0 |
| Length of $P_3$ | 13.3 | 13.5 | 13.0* | 12.6 | 14.0 | 13.0 |
| Width of $P_3$ | 6.0 | 6.6 | 5.6 | 6.1 | 7.0 | 6.2 |
| Length of $P_4$ | 15.1 | 16.0 | 14.6 | 14.6 | 15.9 | 15.1 |
| Width of $P_4$ | 7.6 | 7.3 | 6.9 | 7.4 | 8.3 | 7.4 |
| Length of $M_1$ | 26.3 | 27.5 | 25.8 | 26.8 | 28.8 | 26.8 |
| Width of $M_1$ | 10.3 | 10.7 | 11.0 | 11.7 | 11.9 | 10.8 |
| Length of $M_2$ | 11.8 | | 11.1 | 10.7 | 11.0 | 11.1 |
| Width of $M_2$ | 8.2 | | 8.1 | 8.6 | 8.9 | 7.7 |
| Length of $P_1$ through $M_3$ | 94.1 | 92.2 | 90.0 | 94.1 | 93.6 | 91.5 |
| Length of $P_2$ through $P_3$ | 28.8 | 27.2 | 25.8 | 26.5 | 28.2 | 27.8 |
| Length of $P_2$ through $P_4$ | 45.1 | 44.1 | 41.7 | 43.4 | 45.3 | 43.4 |
| Length of $P_2$ through $M_1$ | 70.3 | 70.0 | 67.4 | 69.9 | 73.3 | 69.3 |
| Length of $P_2$ through $M_2$ | 81.7 | 81.6 | 78.4 | 80.3 | 83.6 | 79.3 |
| Depth of ramus between $P_4$ and $M_1$ | 27.0 | 28.6 | 27.5 | 28.1 | 27.7 | 26.5 |
| Width of ramus between $P_4$ and $M_1$ | 11.5 | 13.1 | 12.1 | 11.7 | 13.6 | 11.7 |

TABLE 2. Measurements (mm.) of left mandibular rami of selected individuals of *Canis lupus* and *Canis niger*. Asterisks indicate inaccurate measurements.

| | *Vulpes palmaria* type. U.S.N.M. 8834 | *Vulpes fulva macroura* M.C.Z. 34097 | *Vulpes fulva abietorum* M.C.Z. 34526, male | *Vulpes fulva abietorum* M.C.Z. 34525, female | *Vulpes fulva* U.S.N.M. 810 | *Vulpes macroura* U.S.N.M. 67584 |
|---|---|---|---|---|---|---|
| Height of jaw at rear of $PM_4$ | 18.0 | 17.3 | 16.0 | 15.9 | 13.5 | 14.0 |
| Thickness of jaw at rear of $PM_4$ | 7.2 | 7.8 | 7.4 | 7.3 | 6.0 | 7.0 |
| Height of jaw at front of $PM_3$ | 14.0 | 13.3 | 14.3 | 13.9 | 11.4 | 13.0 |
| Thickness of jaw at front of $PM_3$ | 7.0 | 6.1 | 6.7 | 7.2 | 6.0 | 6.0 |
| Length of $PM_3$ | 9.1 | 8.5 | 10.6 | 10.1 | 9.0 | 10.0 |
| Width of $PM_3$ | 3.5 | 3.7 | 4.0 | 3.8 | 3.2 | 3.4 |
| Length of $PM_4$ | 10.4 | 10.0 | 11.3 | 11.2 | 9.6 | 10.0 |
| Width of $PM_4$ | 4.3 | 4.7 | 5.2 | 5.0 | 4.1 | 4.0 |
| Side-to-side diameter of socket of canine | 6.5 | 6.1 | 6.6 | 5.7 | 5.1 | |

TABLE 3. Measurements (mm.) of right mandibular ramus of *Vulpes palmaria* and of selected rami of *Vulpes fulva*. Data in the first and in the last two columns from Hay (1917, p. 58).

URSIDAE, Gen. et sp. indet., M.C.Z. 17804, 17805.

Ursid material consists of a left $M^2$, left and right calcanea, right radius lacking distal extremity, left metacarpal I, right metatarsal IV, and a dozen phalanges. As many as three species of bears may have lived in Florida during the Pleistocene: the short-faced bear, *Tremarctos*(?) *floridanus* (Gidley) 1928, the black bear, *Ursus americanus* Pallas 1780, and a "true"[12] *Ursus*. The great homogeneity of the Ursidae as a family together with inadequacy of comparative material (one immature *Tremarctos ornatus*, one immature *Ursus horribilus*, and several *Ursus americanus*) rendered definite identification of the fossils impossible.

[12]Judging from context (Gazin, 1950, p. 401), "true" *Ursus* is intended to apply to *Ursus* minus the black bear (*Euarctos* of authors).

The molar is probably referable to *Ursus* on the basis of its strongly developed internal cingulum, and probably to *U. americanus* on the basis of size. The left metacarpal I is closely comparable to that of a very large *U. americanus*. The radius is slightly larger than that of a large *U. americanus* (M.C.Z. 9331). Comparative measurements (mm.) for the two (fossil first followed by M.C.Z. 9331) are as follows: greatest diameter of proximal articular facet, 41.7 and 38.5; width of shaft at midpoint, 24.0 and 22.7; thickness of shaft at midpoint, 16.8 and 16.1. The calcanea are considerably larger than those of a large *U. americanus*, as indicated by the following measurements:

| | Fossil (left) calcaneum | M.C.Z. 9331 |
|---|---|---|
| Length (parallel to shaft of posterior process) | 85.2mm. | 71.2 |
| Maximum width (parallel to cuboid facet) | 59.7 | 45.3 |
| Width of cuboid facet | 26.2 | 23.3 |

The obliquity of the cuboid facet relative to the shaft of the posterior process is suggestive of an aretothere as opposed to *Ursus*.

*Procyon lotor* (Linnaeus) 1758, M.C.Z. 17818, 17819.

A raccoon indistinguishable from the living North American species is represented by 17 fragmentary mandibular rami, a fragment of a left maxilla with $P^2$, several isolated upper molars, and a number of limb bones. None of the specimens is suggestive of *Procyon nanus* Simpson 1929.

*Mephitis mephitis* (Schreber) 1776, M.C.Z. 17788.

The striped skunk has hitherto been reported in the Pleistocene of Florida only from Saber-tooth Cave, Citrus County, and Seminole Field, Pinellas County. It is now possible to record the species from Melbourne on the basis of a well-preserved left mandibular ramus essentially complete but lacking teeth with the exception of a very worn $M_1$.

*Spilogale ambarvalis* Bangs 1898, M.C.Z. 17787.

The little spotted skunk is recorded on the basis of two left mandibular rami, both quite complete posteriorly but lacking anterior extremities. The dentition is represented in both cases by $P_4$ and $M_1$, slightly worn in one and heavily worn in the other.

*Lutra canadensis* (Schreber) 1776, M.C.Z. 17783, 17784.

Material referable to the modern river otter includes two left maxillary fragments each with $P^4$, fragments of a cranium, three fragmentary mandibular rami, three humeri, two femora, a tibia, an ulna, a radius, and four metatarsals.

*Felis* (*Lynx*) *rufus* (Schreber) 1777, M.C.Z. 17766, 17781, 17782.

The bobcat is represented by a fragmentary right mandibular ramus with $P_3 - M_1$, a fragmentary left ramus with $P_3$ only, isolated left $M_1$ and $P^4$, two calcanea, a humerus, an ulna, two radii, a femur, and two tibiae. Although none of this material is suggestive of a small cat other than a bobcat, Gazin's (1950, p. 402) record of a jaguarundi or margay type of cat at Melbourne is highly provocative. A re-examination of the fossils from other Florida localities that have been previously assigned to *Felis* (*Lynx*) *rufus* may reveal additional evidence relevant to this zoogeographically interesting possibility.

*Felis* sp., cf. *F.* (*Puma*) *inexpectata* (Cope) 1895, M.C.Z. 17791.

In the Singleton Collection are six phalanges, a right astragalus, a left radius, and two distal fragments of metapodials, none of which can be distinguished from comparable elements of Recent *Felis concolor*. These bones may tentatively be referred to *Felis inexpectata*, regarded by Simpson (1941, p. 23) as inadequately distinguished from *F. concolor*.

*Monachus tropicalis* (Gray) 1850, M.C.Z. 4439, Figs. 4, 5.

In the Singleton Collection are two bones labeled "sea lion or fur seal." One of these proved to be the left first metatarsal of an alligator (renumbered M.C.Z. 2811). The second bone does indeed belong to a pinniped, but not to an otariid as the original label states. The bone in question is the proximal phalanx of the right hallux of *Monachus tropicalis*. This identification is based on comparison of the fossil with skeletons of the following living species: *Monachus tropicalis, Phoca groenlandica, P. vitulina, Erignathus barbatus, Halichoerus grypus, Cystophora cristata, Mirounga angustirostris, Callorhinus ursinus, Eumetopias jubata, Zalophus californianus, and Odobenus rosmarus*. The proximal phalanx of the hallux in *Monachus tropicalis* was found to be very distinctive.

The shape and cross-section of the shaft is sufficient to separate the fossil from otariids and odobenids. In the fossil (and in all

phocids examined) the shaft has a ventro-medial sharp edge producing an asymmetrical cross-section, whereas in otariids the shaft is much flattened dorso-ventrally with a nearly symmetrical cross-section and in *Odobenus* the shaft is thickened dorso-ventrally with an elliptical cross-section. The extremities of the bone in *Odobenus* are enlarged and knoblike in comparison with other pinnipeds.

In all phocids examined excepting *Monachus* and the fossil there is a well-developed longitudinal channel extending the length of the ventral surface of the shaft. This channel is well developed only at the proximal end in *Monachus* and in the fossil, the remainder of the shaft having a flat to gently convex ventral surface (Fig. 5, right).

In all phocids excepting *Monachus* and the fossil the shaft of the bone appears to be twisted, a feature readily apparent upon comparison of the relative orientation of proximal and distal articular facets. In *Monachus* and the fossil the distal articular facet extends only slightly onto the dorsal and ventral surfaces whereas in other phocids it extends considerably onto these surfaces (Figs. 4 and 5). The proximal articular surface in phocids is subcircular in outline with a deep ventral indentation resulting in a shape resembling a robust letter U (Fig. 4). *Monachus* and the fossil differ from other phocids examined in having the lateral arm of the U much larger than the medial and the medial arm deflected distad relative to the plane of the articular facet as a whole.

The fossil is matched almost perfectly by the corresponding bone of an apparently old individual of *Monachus tropicalis* (A.M.N.H. 10421, Figs. 4C, 5C). In both bones the epiphyses are completely closed. These are among the last to fuse in the skeleton as closure occurs successively from proximal to distal elements in the limbs (King, 1956, p. 250). Comparative measurements (mm.) of the two (fossil first, followed by A.M.N.H. 10421) are as follows: length, 91.9 and 92.3; maximum breadth of shaft measured parallel to ventral surface, 23.0 and 24.1; minimum breadth of shaft, 14.3 and 14.4; maximum thickness of shaft, 17.6 and 17.4; minimum, 8.8 and 8.5. The two specimens are similar also in the presence of a very strong rugosity on the

anteromedial surface of the proximal end of the shaft (Figs. 4, 5).

The present record is well outside the known historic range of *Monachus tropicalis*. The monk seal has been recorded from southernmost Florida and was abundant in the Bahamas as late as 1707 (G. M. Allen, 1942, pp. 453, 454). The northernmost point in the Bahamas is Matanilla Reef at 27°25′N. as compared to Melbourne at 28°5′N. The monk seal was so quickly decimated at the hands of modern man that its pre-Columbian range cannot be determined, but it may well have included the Melbourne area.

Of considerable interest in connection with past distribution are the left and right auditory regions (presumably from the same individual) of *M. tropicalis* preserved in the mammal department of the museum (M.C.Z. 8741). Both specimens include the glenoid fossa, auditory bulla, mastoid, and petrosal. Unfortunately, locality and horizon are unknown, the only data accompanying the specimens being "South Carolina?" and "R. W. Gibbes collection?" Gibbes (1809-1866) was a life-long resident of Columbia, South Carolina, and his large collections derive almost entirely from the southeastern United States. If the specimens are from his collection as seems probable, they furnish a record (Pleistocene?) for the monk seal considerably north of its known historical range.

## Proboscidea

*Mammut americanum* (Kerr) 1792, M.C.Z. 5837, 17806-17809, 17811-17815, 17829-17832, 17834-17837.

The American mastodon is represented by some 24 molars and by an immature right mandibular ramus. Most interesting of the teeth are two first lower deciduous molars, one deeply worn (17814) and one unworn (17815).

*Mammuthus* sp. indet., M.C.Z. 2013, 5838, 17820, 17821, 17823-17828.

Twelve isolated molars, mostly fragmentary, and a right mandibular ramus with $M_3$ are referred to the mammoth. The isolated molars are inseparable from the common *Mammuthus columbi*, and may be referred to that species. The $M_3$ in the mandible has not less than 19 enamel plates and technically should probably

be referred to *M. imperator*. Unidentified and uncatalogued proboscidean material includes a rib and tusk fragments.

## Perissodactyla

*Equus* sp. indet., M.C.Z. 2034-2038, 2041, 2042, 2051-2056, 2058-2065, 3348, 5911.

The genus *Equus* is represented by 233 isolated cheek teeth, 43 incisors (M.C.Z. 2051), a left mandibular ramus with $P_2 - M_2$ (M.C.Z. 2052), a fragment of a right ramus with $P_2$ (M.C.Z. 2052), a complete mandible with all molariform teeth, right $I_2$, and left $C_1$ (M.C.Z. 3348), a left ulna, and miscellaneous foot material. Savage (1951) is followed in withholding specific identification pending a revision of named species.

*Tapirus* sp., cf. *T. veroensis* Sellards 1918, M.C.Z. 5839, 7154-7158.

The Singleton Collection contains a considerable amount of tapir material including approximately 64 isolated but complete cheek teeth and eight fragmentary tooth-bearing elements each with one or more teeth in place but only one (M.C.Z. 5839) with a complete cheek tooth row. Noteworthy among these is a mandible of a very young individual with $DP_2$, $DP_3$, and the roots of $DP_4$ on the left side, and with $DP_2 - DP_4$ on the right. The symphysis remains intact, but anterior teeth have been lost, whereas the more posterior teeth remain unerupted.

## Artiodactyla

*Mylohyus* sp. indet., M.C.Z. 17871-17873.

Fourteen molariform teeth and two lower canines are referred to *Mylohyus*. No attempt has been made to identify these teeth specifically.

*Platygonus* sp. indet., M.C.Z. 17874.

The genus *Platygonus* is represented by five characteristic cheek teeth. Also representing the Tayassuidae but not further identified are two calcanea, a radio-ulna, a phalanx, and three astragali.

*Tanupolama* sp., cf. *T. mirifica* Simpson 1929, M.C.Z. 17816, 17817.

A camel comparable in size to *T. mirifica* is represented by three astragali, seven cheek teeth, and one incisor. Among the molariform teeth is the left $P^3$ illustrated by Bader (1957, p. 60, fig. 3).

*Odocoileus virginianus* (Boddaert) 1784, M.C.Z. 5910, 17838-17864.

Abundant remains of the white-tailed deer include eight fragmentary mandibular rami, 175 isolated teeth, and almost every part of the skeleton. Three of the mandibular rami (M.C.Z. 5910, 17839, 17840) have been worked in identical fashion by man. Beginning under $P_2$ and continuing posteriorly, the ventral border of each jaw has been beveled off smoothly parallel to the dorsal border of the ramus. No specimens suggestive of *O. sellardsiae* Hay 1917 were found in the collection. J. T. Gregory (in Rouse, 1951, p. 164) has described Hay's type description as "unconvincing," an opinion in which the present author heartily concurs.

*Bison* sp. indet., M.C.Z. 2015, 2016, 2026, 2029, 2032, 2033, 17875.

The following material is referred to the genus *Bison*: 12 vertebrae, one scapula, two humeri, two radii, one ulna, two tibiae, two metapodials, two astragali, 59 isolated cheek teeth, and one left mandibular ramus with $P_4 - M_3$. The mandibular ramus is very similar to the one from Bradenton figured by Simpson (1930, p. 12, fig. 7) and identified by him as *B. latifrons*. Comparative measurements (mm.) are as follows:

| | A.M.N.H. 26831 (from photograph) | M.C.Z. 17875 |
|---|---|---|
| Length $M_1 - M_3$ | 113.2 | 111.3 |
| Length $P_2 - M_3$ (alveoli) | 180.0 | 179.2 |

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## APPENDIX: SPECIES LIST OF THE MELBOURNE MAMMALIAN FAUNA

The following list of species recorded from the Pleistocene of Melbourne is based on the papers of Simpson (1929A, p. 268) and Gazin (1950, pp. 397-404), and on the present study. Forms represented in the Singleton Collection are designated by an asterisk (*). Several exotic records listed in preliminary faunal lists for Melbourne but not followed up in later publications are excluded here. These include *Microtus*, antelope?, and reindeer? (Gidley, *in* Cooke, 1926, p. 445) and *Taurotragus?* (Gidley, *in* Hay, 1927, p. 274).

**Didelphis marsupialis* Linnaeus 1758 — opossum
**Scalopus aquaticus* (Linnaeus) 1758 — eastern mole
**Blarina brevicauda* (Say) 1823 — short-tailed shrew
**Molossides floridanus* G. M. Allen 1932 — molossid bat
**Homo sapiens* Linnaeus 1758 — man (artifacts only in Singleton Collection)
*Megalonyx jeffersonii* (Desmarest) 1822 — ground sloth
**Megalonyx* cf. *wheatleyi* Cope 1871 — ground sloth
**Paramylodon* cf. *harlani* (Owen) 1840 — ground sloth
**Dasypus bellus* (Simpson) 1929 — armadillo
**Chlamytherium septentrionalis* (Leidy) 1890 — giant armadillo
*Boreostracon floridanus* Simpson 1929 — glyptodont
*Sylvilagus floridanus* (J. A. Allen) 1890 — cottontail rabbit
**Sylvilagus palustris* (Bachman) 1837 — marsh rabbit
*Sylvilagus palustrellus* Gazin 1950 — pygmy marsh rabbit
**Geomys pinetis* Rafinesque 1817 — "salamander," gopher
*Castoroides* cf. *ohioensis* Foster 1838 — giant beaver
**Oryzomys palustris* (Harlan) 1837 — rice rat
**Peromyscus gossypinus* (Le Conte) 1853 — cotton mouse
**Sigmodon hispidus* Say and Ord 1825 — cotton rat
**Neotoma floridana* (Ord) 1818 — wood rat
**Synaptomys australis* Simpson 1928 — southern bog lemming
**Neofiber alleni* True 1884 — round-tailed muskrat
*Neochoerus pinckneyi* (Hay) 1923 — giant capybara
*Hydrochoerus* sp. — capybara

Gazin (1950) does not list this genus, and it is barely possible that the material furnishing the basis for the record would now be referred to *Neochoerus*. However, Simpson (1929A, p. 268) lists *Hydrochoerus* and he would almost certainly have altered the name to *Neochoerus* (erected in 1926 by Hay) had the material been referable to the giant capybara.

*Canis* cf. *latrans* Say 1823 — coyote
*Canis* cf. *lupus* Linnaeus 1758 — wolf
*Aenocyon* cf. *ayersi* (Sellards) 1916 — giant wolf
*Urocyon* cf. *cinereoargenteus* (Schreber) 1775 — gray fox
*Vulpes* ?*palmaria* Hay 1917 — "red" fox
*Tremarctos(?) *floridanus* (Gidley) 1928 — short-faced bear
*Ursus americanus* Pallas 1780 — black bear
*Ursus* sp. — large "true" *Ursus* (see Gazin, 1950, p. 401)
*Procyon lotor* (Linnaeus) 1758 — raccoon
*Spilogale ambarvalis* Bangs 1898 — little spotted skunk
*Mephitis mephitis* (Schreber) 1776 — striped skunk
*Lutra canadensis* (Schreber) 1776 — river otter
*Felis (*Puma*) cf. *inexpectata* (Cope) 1896 — puma
*Felis (*Herpailurus* or *Noctifelis*) sp. — margay or jaguarundi-like cat
*Felis (*Lynx*) *rufus* (Schreber) 1777 — bobcat
*Panthera (*Jaguarius*) *augusta* (Leidy) 1872 — extinct jaguar
*Smilodon* cf. *floridanus* (Leidy) 1889 — saber-toothed cat
*Monachus tropicalis* (Gray) 1850 — West Indian monk seal
*Mammut americanum* (Kerr) 1792 — American mastodon
*Mammuthus columbi* (Falconer) 1857 — Columbian mammoth
?*Mammuthus imperator*? (Leidy) 1859 — imperial mammoth
*Equus* sp. — horse
*Tapirus veroensis* Sellards 1918 — Vero tapir
*Platygonus*, near *P. compressus* Le Conte 1848 — extinct peccary[13]
*Platygonus* cf. *cumberlandensis* Gidley 1920 — extinct peccary
*Mylohyus gidleyi* Simpson 1929 — extinct peccary
*Mylohyus* cf. *exhortivus* Gidley 1920 — extinct peccary
*Tayassu* (including *Pecari*) sp. — peccary

A record of *?Pecari* sp. listed by Simpson (1929a, p. 268) may indicate the presence of a second species of *Tayassu*, related to the living collared peccary.

*Tanupolama mirifica* Simpson 1929 — extinct camelid
*Odocoileus virginianus* (Boddaert) 1784 — white-tailed deer
*Cervus*? sp. — large wapiti-like deer
*Bison* sp. — bison

[13] Peccary remains in the Singleton Collection are identifiable to genus only.

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Figure 3. Lingual view of fragmentary left mandibular ramus of *Dasypus bellus*, M.C.Z. 17803. X3.

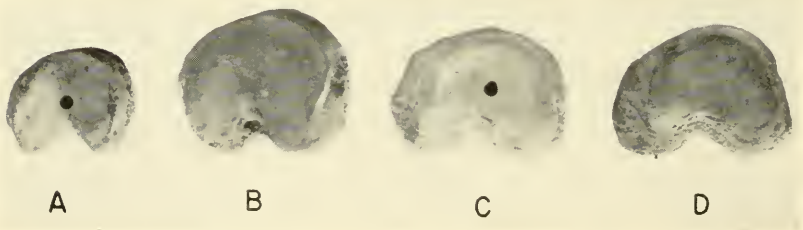


Figure 4. View of proximal articular facets of proximal phalanges of right hallux of *A*, *Phoca vitulina* (M.C.Z. 1738); *B*, *Cystophora cristata* (M.C.Z. 1084); *C*, *Monachus tropicalis* (A.M.N.H. 10421); *D*, *Monachus tropicalis* (M.C.Z. 4439, fossil). X1.

Figure 5. Dorsal (*on left*) and ventral (*on right*) views of proximal phalanges of right hallux of *A*, *Phoca vitulina* (M.C.Z. 1738); *B*, *Cystophora cristata* (M.C.Z. 1084); *C*, *Monachus tropicalis* (A.M.N.H. 10421); *D*, *Monachus tropicalis* (M.C.Z. 4439, fossil). X approximately 3/4.

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## Part. 1. Cranial Differences Between *Python sebae* and *Epicrates cenchris*.

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No. 8 — *Studies on the Morphology and Function of the Skull in the Boidae (Serpentes)*

# Part 1. Cranial Differences between *Python sebae* and *Epicrates cenchris*

By T. H. Frazzetta
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## INTRODUCTION

Classically, the Boidae was considered to consist solely of the two subfamilies Pythoninae and Boinae. The presence of supraorbital bones in the former, and their absence in the latter served to distinguish the two groups. However, Hoffstetter (1946, 1955) and Brongersma (1951) have removed several genera from the "old" Boinae and grouped them in the subfamilies Bolyerinae, Erycinae, and Tropidophinae, while more recently Romer (1956) has proposed a classification of the Boidae which has again altered the taxonomy of the primitive snakes in several important respects. He has removed the genus *Loxocemus* from the Pythoninae and placed it with the Aniliidae, and has considerably modified the content of the remaining subfamilies: Two genera from the Boinae of other authors together with the bolyerine genera were grouped to compose the Sanziniinae; another boine genus, *Candoia* (= *Enygrus*; I am using the nomenclature of Foreart, 1951), has been placed in the Erycinae; and the Tropidophinae have been lumped with the remaining Boinae. These changes in the classification in the Boidae are diagrammed in Figure 10.

The present paper is the first of a series of publications that will deal with the boid skull in terms of morphology, function, and evolution. The original point of departure of these studies was an examination of cranial kinesis with special reference to burrowing forms, but so much information has been gathered about non-burrowing types that these will be considered first.

Rapid and marked changes in the taxonomy of primitive snakes have meant considerable shuffling of genera with respect to the higher taxonomic categories. Today, the use of a formal family or subfamily name in connection with the primitive

snakes leads only to confusion unless specific definitions of the terms are given. Romer's classification appears unsuitable in various respects and therefore cannot represent a sound foundation. Furthermore, I cannot allow myself to adopt any classification other than Romer's (which is the latest) without *first* presenting the evidence upon which my judgment is based. Under these rather awkward circumstances, it is necessary to select, for purposes of the initial descriptions and discussion, genera which possess common features and which can be distinguished from all other forms. This done, comparisons can be made and the taxonomic situation can be evaluated.

It seems advisable to abandon, for the present, the use of any formal family or subfamily names for the group of snakes selected for discussion; hence, I refer to this group as the boide snakes. These are the classical Boidae minus the Tropidophinae of Brongersma and the Bolyerinae of Hoffstetter. Within this group, two subgroups can tentatively be recognized. One of these is characterized by the presence of supraorbital bones, the other by the absence of these elements. I shall refer to these subgroups, respectively, as the python-like and boa-like snakes, or, more simply, pythons and boas. These subgroups correspond to the Pythoninae and Boinae of Brongersma (1951) but not to those of other authors (see Fig. 10).

The boide snakes in the sense of the present paper can be distinguished from other primitive snakes on the basis of a number of morphological characters. From the Tropidophinae of Brongersma they differ in the posterior end of the dentary not lying well in advance of the vertical lamellae of the compound bone, in the more developed outer lamella (surangular process), and in visceral characters (Cope 1900, Brongersma 1951). They differ from the Bolyerinae of Hoffstetter in the possession of two, rather than four, maxillary elements (Hoffstetter 1946, Anthony and Guibé 1952). The boide snakes differ from the remaining groups of primitive snakes in that the supratemporal bones are well developed and are not incorporated into the braincase, in that the maxilla is never suturally united with the premaxilla, and in that the posterodorsal and posteroventral rami of the dentary appear very nearly of equal length when viewed laterally.

In the present paper the skull of a python-like species, *Python sebae,* and a boa-like form, *Epicrates cenchris,* are described and compared. These descriptions will then be used to frame a tabular comparison of the pythons and boas with the aid of which other genera can be compared and contrasted.

## ACKNOWLEDGMENTS

Numerous individuals have generously offered valuable advice and criticisms. I especially wish to thank Dr. Ernest E. Williams for countless aids. I am also deeply indebted to the following for their suggestions and encouragement: Dr. Max K. Hecht, Mr. Bryan Patterson, Dr. Samuel B. McDowell, Dr. Carl Gans, Dr. Karl F. Koopman, and Dr. James A. Oliver.

Sincere gratitude is expressed to the following persons for the loan of specimens: Mr. Charles M. Bogert and Dr. Richard G. Zweifel of the American Museum of Natural History, Dr. Doris M. Cochran of the United States National Museum, Dr. Ernest E. Williams of the Museum of Comparative Zoology, and Mr. Bruce B. Collette, Mr. John B. Swinford, Dr. Charles A. Triplehorn, and Mr. Theodore O. Hendrickson for specimens from their private collections.

## THE SKULL OF *PYTHON SEBAE*

The premaxilla (= the two fused premaxillae) is the anteriormost bone of the skull (Figs. 1*A*, 1*B*, 2*A*, 3*A*, 3*B*). It is transversely expanded anteriorly, and bears four teeth. The transverse portion of the bone occupies a position nearly directly in front of the other snout bones. A pair of small channels pierces the transverse part of the premaxilla (see Figs.); the axis of each cylindrical lumen is directed downward and a little forward. Posteriorly, the premaxilla is produced into two processes, an upper laterally-compressed process (the processus nasalis, Fig. 3*A*, *B*, *pn*) which passes backwards between the two descending lamellae of the nasals, and a lower bifurcate one (processus palatini, Fig. 3*A*, *B*, *pp*), the rami of which extend to the anterior tips of the vomers.

The paired nasal bones each consist of a broad sheet lying in a horizontal plane, and a descending lamella that meets the hori-

zontal sheet at right angles along its medial border. Anteriorly, the descending lamellae of the two nasals embrace the processus nasalis of the premaxilla.

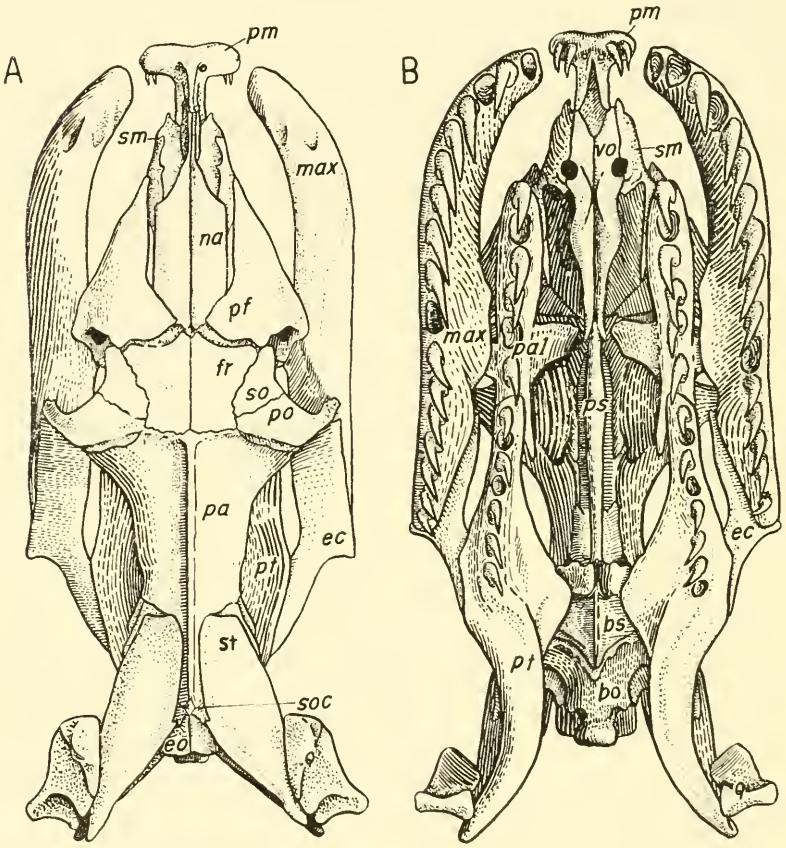


Fig. 1. *Python sebae*. Views of skull: *A*. dorsal, *B*. ventral. For abbreviations see page 470.

The septomaxillary bones lie against the descending lamellae of the nasals. They are significantly wider than the greatest width of the nasals. The outer edge of each septomaxilla, with

the exception of its most anterior part, is curled upward to form a trough (see Figs. 1*A*, 4*A*, 4*D*). At the level of the forward ends of the palatines, the outer edge of each septomaxilla expands laterally to form a blunt process (Figs. 4*A*, 4*D*), and tapers caudally to produce a delicate spine.

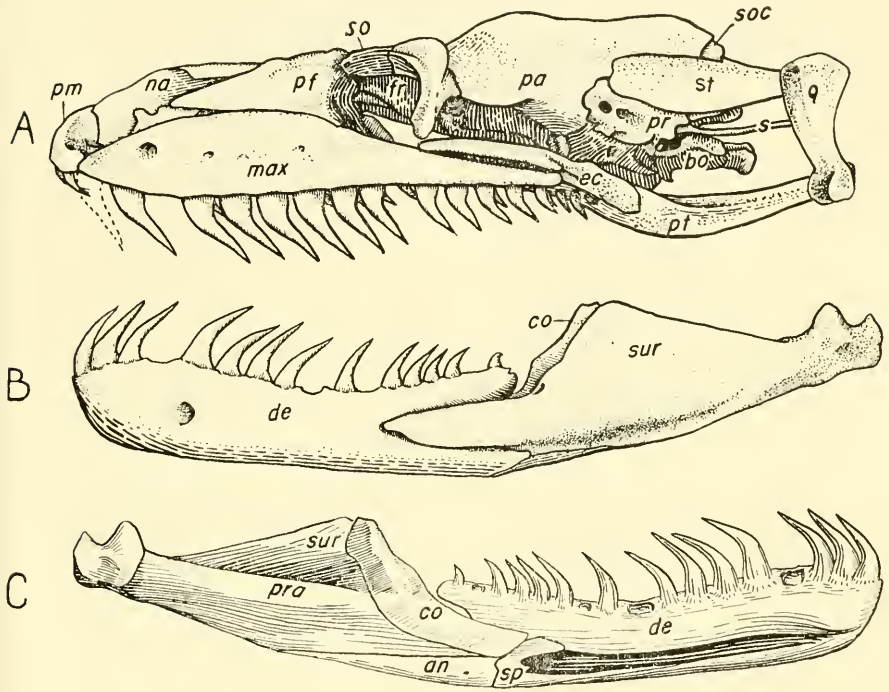


Fig. 2. *Python sebae*. *A*. lateral view of skull. *B*. lateral, *C*. lingual views of left mandible. For abbreviations see page 470.

The vomers adhere to the inferior surfaces of the septomaxillaries, and extend forward to contact the processus palatini of the premaxilla, and backward to reach the frontals and parasphenoid. Behind the septomaxillaries, each vomer takes the form of a narrow horizontal sheet with a vertical lamella arising along its medial edge (see Figs. 1*B* and 4*A*). Caudally, the

horizontal portion tapers gradually, losing its distinction from the ascending lamella. The lamellae of both vomers are in contact throughout most of their length, but their posterior ends are spread apart to admit the spine-like tip of the parasphenoid (Fig. 4*A*).

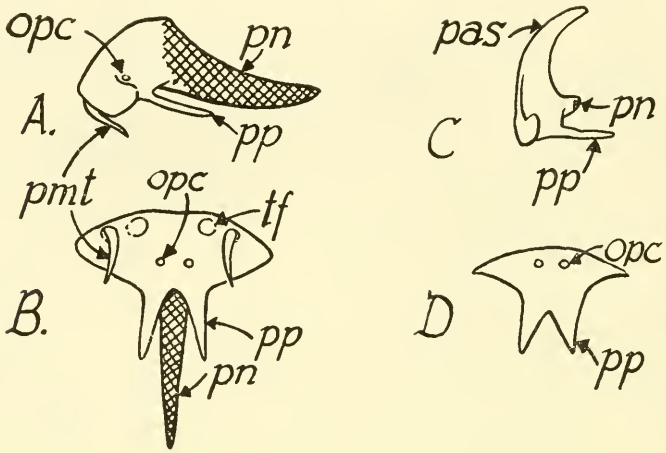


Fig. 3. Lateral and ventral views of premaxillary bones in *Python*, *A* and *B;* and in *Epicrates, C* and *D*. Cross-hatched areas are those which are hidden from view by nasal lamellae when *in situ*. For abbreviations see page 470.

The seven-bone complex, consisting of the fused premaxillae, nasals, septomaxillaries, and vomers, will be referred to as the "snout complex" (Fig. 4*A*). This collective term is convenient; the complex constitutes a functional unit inasmuch as none of the individual bones moves relative to another.

Posterodorsally, the snout complex forms a movable articulation with the frontals. Here the descending lamellae of the nasals diminish; the bones lie upon the medial superior surfaces of the frontals near their forward edges (Figs. 4*A* and 4*B*).

The frontals are paired elements that may be described as roughly box-shaped. They are flattened above and slightly concave laterally. The side wall of each frontal descends rather

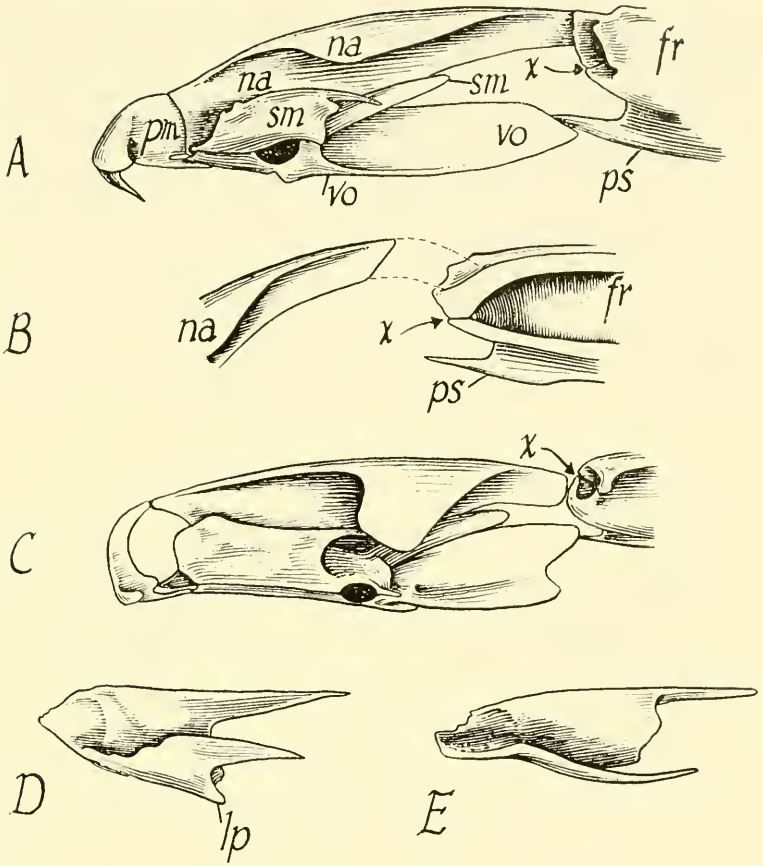


Fig. 4. *A.* lateral view of snout bones and their articulation with frontals (prefrontals having been removed) in *Python*. *B.* Detail of naso-frontal articulation in *Python;* here the left frontal has been removed, revealing the medial aspect of the right frontal; the posterior ends of the nasals have been tilted up and away from their region of normal articulation with the frontal(s), as indicated by the broken lines. *C.* Lateral view of snout bones and their articulation with frontals (prefrontals having been removed) in *Epicrates*. *D* and *E*. Dorsal views of left septomaxillae in *Python* (*D*) and in *Epicrates* (*E*); the anterior ends are to the left of the figure. For abbreviations see page 470.

abruptly and forms part of the inner wall of the orbit; its vertical dimension is nearly equal to the dorsal width of the bone. Below, the frontals articulate with the parasphenoid which runs along their median ventral suture. The anterior faces of the frontals are pierced by foramina for the two olfactory tracts that here pass out of the braincase to the snout region. Examination of the medial rim of either of these foramina discloses evidence of a suture separating the medial frontal wall into upper and lower horizontal portions. At the area of articulation with the nasals (Figs. 4*B* and 5*A*), there is a slight anterior expansion of the medial superior surfaces of the frontals; the area of naso-frontal articulation is thus at the upper frontal portions and somewhat above the two olfactory foramina (as noted by Hoffstetter 1939). Dorsally, the lateral edges of the frontals join the

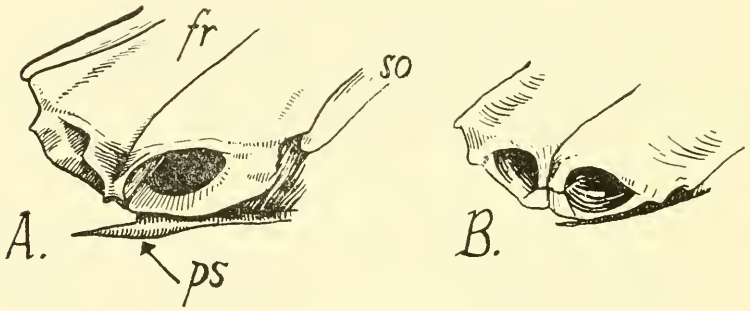


Fig. 5. Oblique views of anterior faces of frontals and associated elements. *A. Python. B. Epicrates.* For abbreviations see page 470.

flakelike supraorbitals; the latter bones roof the orbits and continue medially for a short distance beneath the frontals (Figs. 1*A* and 2*A*).

The prefrontals are roughly triangular in form, their apices projecting forward. Each prefrontal expands medially to lie upon a portion of the frontal just lateral to the naso-frontal articulation. The prefrontals do not meet dorsally, nor do they substantially overlap the outer margins of the nasals. They descend to articulate with the palato-maxillary arches and, in this manner, form the anterior walls of the orbits. The dorso-

medial edge of the orbital portion of each prefrontal expands to fit into a shallow recess in the side wall of the frontal, thus forming a movable articulation between the prefrontal and the braincase. The anteriormost tip of the supraorbital turns downward and actually runs slightly beneath the lateral corner of the prefrontal-frontal joint. In the anterior orbital region, the prefrontal is perforated by the lachrymal foramen (Fig. 6*A*).

Behind the frontals is the large parietal, the dorsal and lateral surfaces of which serve for the origin of powerful jaw muscles of the adductor series. Dorsally, the parietal bears a medial longitudinal crest for muscle attachment.

The postorbitals (Figs. 7*A*, *B*, *C*) are massive and bilobed dorsally. The anterior lobe makes contact with the frontal, parietal, and supraorbital bones and turns ventrad to run a short distance beneath the two former elements. The posterior lobe lies upon the parietal, not meeting the frontal and supraorbital bones (see Figs. 1*A*, 7*A*, 7*B*, 7*C*). Ventrally, the postorbitals come very nearly into contact with the outer rami of the palatomaxillary arches, to which they attach by ligaments.

Lying scalelike upon the upper rear portion of the parietal are the flat and straight paired supratemporal (= squamosal, tabular) bones. They serve to suspend the quadrates from the braincase.

Each quadrate is short (less than ¼ of the distance from the premaxilla to the occipital condyle) and nearly vertical in position. Dorsally, it enters a movable articulation with the supratemporal. Ventrally, it articulates with the articular portion of the compound bone of the mandible, and ventromedially it joins the posterior tip of the pterygoid (Figs. 1*A*, 1*B*, 2*A*).

The palato-maxillary arches are each composed of a medial ramus and a lateral ramus (see Fig. 1*B*). The medial ramus consists of the toothed pterygoid and palatine bones, while the lateral ramus is composed of the edentulous ectopterygoid and toothed maxilla.

The lateral processes of the palatines form articulations with the prefrontals and the inner expansions of the maxilla; the thick medial processes extend dorsad toward the inferior surface of the braincase (Fig. 1*B*). Posteriorly, the palatines continue backward as spines which run along the dorsomedial

surfaces of the pterygoids. A longitudinal channel perforates each palatine at the base of its lateral process (Fig. 6*A*).

The ectopterygoid bones arise from the lateral edges of the pterygoids. Anteriorly, they articulate with the upper surfaces

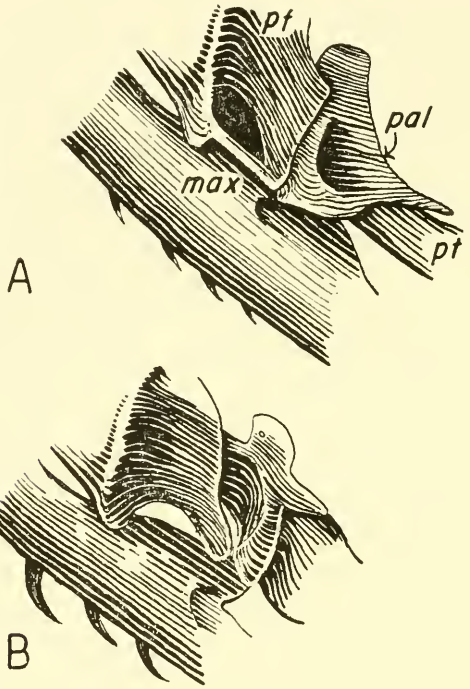


Fig. 6. Bones of the floor and anterior wall of the left orbit, as seen from behind and above in a python-like snake (*A*), and in a boa-like snake (*B*). For abbreviations see page 470.

of the posterior ends of the maxillary bones (Figs. 1 and 2*A*).

Each maxilla articulates with the lower portion of a prefrontal, and sends a broad medial process beneath this bone to the palatine (Fig. 6*A*).

The two conspicuous basipterygoid (basitrabecular) processes of the basisphenoid bone make contact with the pterygoids from

above. The basisphenoid also bears a prominent ventromedian crest for the origin of muscles that pass obliquely backward to insert upon the pterygoids. If the total length of the skull is defined as the longitudinal distance from the premaxilla to the level of the quadrate-pterygoid joint, then the distance from

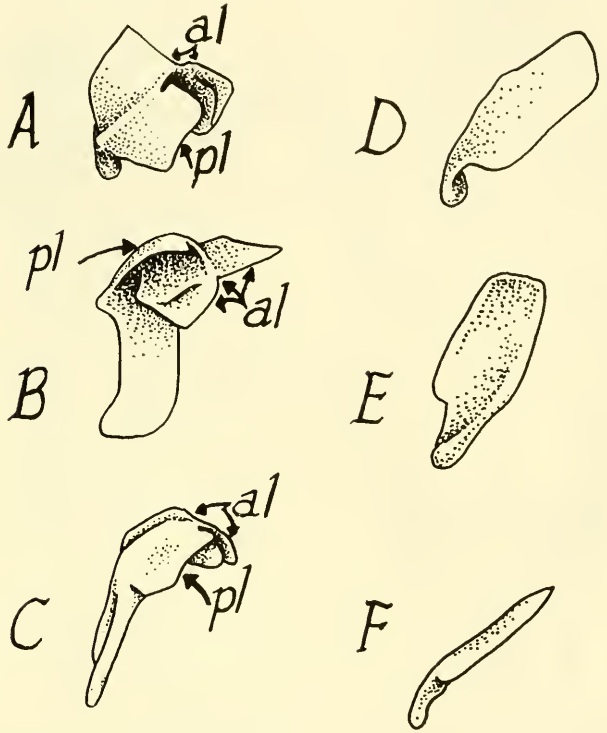


Fig. 7. Views of postorbital bones in *Python* (*P. molurus*): *A.* dorsal, *B.* medial, *C.* posterior; and in *Epicrates* (*E. cenchris*): *D.* dorsal, *E.* medial, *F.* posterior. For abbreviations see page 470.

the basipterygoids to the posterior limit of the skull is considerably less than one-half of the total length.

Behind the basisphenoid is the basioccipital, which contributes posteriorly to the medial portion of the occipital condyle. The outer portions of the condyle are formed by the exoccipitals

which meet one another above the foramen magnum and exclude the supraoccipital from its rim. The supraoccipital lies upon the exoccipitals and behind the parietal. Posteriorly, it bears two

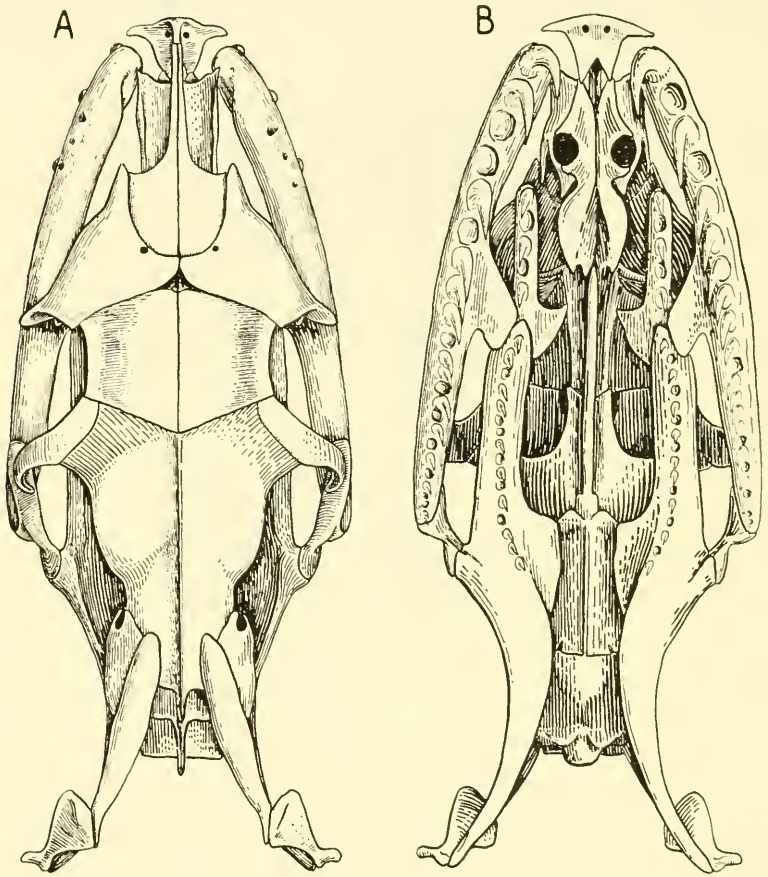


Fig. 8. *Epicrates cenchris.* Views of skull: *A.* dorsal, *B.* ventral.

short, low crests that meet anterodorsally but diverge posteroventrally.

The prootics are surrounded by the basisphenoid, basioccipital, parietal, and exoccipital bones (the latter indistinguishably fused

with the opisthotics). The foramen ovale pierces the prootic-exoccipital suture. The stapes passes backward out of this foramen and bears a small pad of cartilage upon its distal tip. This cartilage connects with a tuberosity of the inner side of the quadrate by means of an elastic band of tissue.

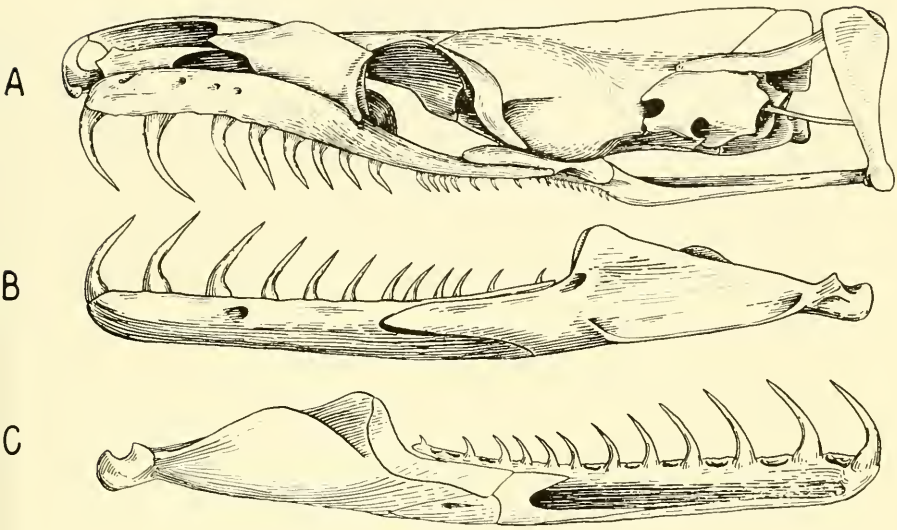


Fig. 9. *Epicrates cenchris*. *A*. lateral view of skull. *B*. lateral and *C*. lingual views of left mandible.

As in all snakes, the mandibles are not united by a firm symphysis, but are free distally. Each mandibular ramus is composed of five distinct bones: dentary, splenial, angular, coronoid, and compound bone. The last has been often referred to in snakes as the articular, but, because it is actually formed in the boide snakes by the fusion of the surangular, prearticular, and articular, the term "compound bone" is more applicable. From each compound bone two lamellae arise: an outer surangular process and an inner prearticular process. The surangular lamella rises considerably above the prearticular process. A foramen pierces the surangular lamella (see Fig. 2*B*).

## THE SKULL OF *EPICRATES CENCHRIS*

The overall aspects of the skulls of *Python sebae* and *Epicrates cenchris* are essentially similar. For this reason, it is impractical to describe each structure of *Epicrates* in the same detail in which those of *Python* were considered. Thus, many of the cranial structures which are sufficiently alike in both forms will be omitted from mention in the following description.

The premaxilla is like that of *Python* in that it is expanded transversely and bears a processus nasalis and a processus palatini. However, it is conspicuously unlike that of *Python* in several particulars: (1) premaxillary teeth are absent (Fig. 3*D*); (2) the processus nasalis is tiny (Fig. 3*C*); (3) there is an additional process which rises vertically to meet the anterodorsal corners of the nasals; this shall be referred to as the ascending process of the premaxilla (Fig. 3*C*); and (4) the paired premaxillary channels are directed downward and backward.

In *Epicrates,* the septomaxillae are not wider than the nasals, and it is their most anterior portions that are curled upward (Figs. 4*C* and 4 *E*). Their outer edges terminate caudally in a spine as in *Python* but are not produced laterally into the blunt process seen in that genus (Figs. 4*C* and 4*E*). The vomers are like those of *Python* except that they become wider ventrocaudally, and the distinction between the horizontal and ascending portions is conspicuous throughout the lengths of the bones.

Unlike the condition in *Python*, the upper horizontal portions of the frontals do not enter into the naso-frontal joint. In *Epicrates*, the lower portions are produced forward as apophyses, and it is these with which the nasals articulate (see Figs. 4*C* and 5*B*).

The frontals are comparatively wide in *Epicrates*; in the absence of separate supraorbital bones, they are expanded to roof the orbits. Dorsally, each bears a shallow depression which runs the length of the bone. Below, the inferior surface of each is horizontal in the orbital region and gradually descends medially to meet its fellow.

The prefrontals are very similar in shape to those of *Python*, despite some noteworthy differences. The frontal recess which receives the prefrontal process is not laterally placed against

the side wall of the braincase as in *Python*; due to the lateral expansion of the frontals over the orbit, this recess occupies a position beneath this shelflike extension, and thus its concavity opens more ventrally in *Epicrates*. The area of ginglymoid prefrontal-frontal articulation reaches to the anterolateral cor-

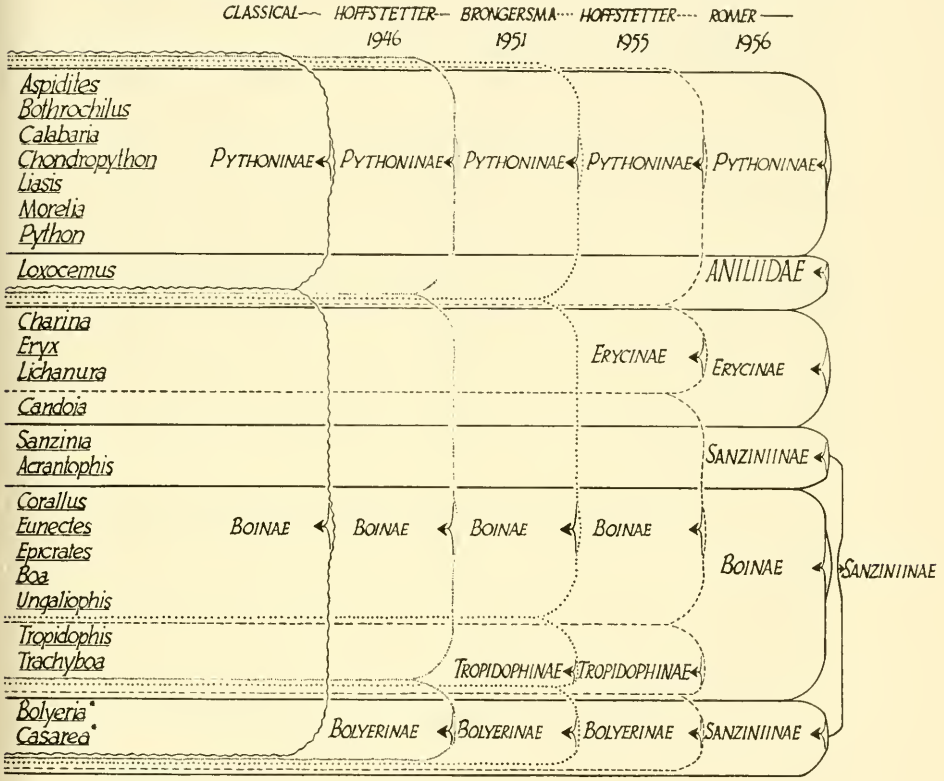


Fig. 10. Classification changes in the Boidae. Genera marked with an asterisk have not been examined for the present paper.

ner of the frontal. Dorsally, each prefrontal expands medially to meet its fellow over the nasal bones, and runs forward to closely overlap the lateral margins of the latter. In the anterior orbital region, the lachrymal foramen is represented by a deep

emargination of the prefrontal from below (see Fig. 6*B*).

The postorbitals (Fig. 7*D*, *E*, *F*) appear much less elaborate than those of *Python*; in particular, there is no trace of bilobation. The sole area of contact of these bones with the braincase is with the dorsal surface of the latter. Each postorbital lies upon the parietal and extends forward to the posterior margin of the frontal. Beneath the postorbitals, the parietal is emarginate just behind the frontals.

In *Epicrates*, the supratemporals are slender and are curved upward.

The quadrates are long (greater than ¼ of the distance from the premaxilla to the occipital condyle).

The palato-maxillary arches of *Python* and *Epicrates* are similar in essentials. Most of the differences in the relative sizes and shapes of the constituent bones are readily seen by comparing the figures. Three features are worthy of mention. The lateral edge of the base of the outer palatine process is emarginate, thus obliterating the outer rim of the palatine channel (see Fig. 6*B*). Moreover, the palatine lacks the backward spine which is so prominent in *Python*. Reference to Figure 8*B* will reveal that in *Epicrates* the inner process of the maxilla is "swept" backward.

The basipterygoid processes are relatively anterior in position. They are located about halfway between the premaxilla and the posterior limit of the skull (the level of the quadrate-pterygoid joint).

Unlike the condition in *Python*, the supraoccipital bone of *Epicrates* bears a single median crest, which extends backward from the caudal edge of the parietal crest.

Along the ventrolateral edge of the compound bone, there arises a thin shelf of bone. In *Epicrates*, in contrast to *Python*, the inner or prearticular lamella is well developed, and is visible from lateral view.

## TABULAR COMPARISON

*Python sebae* exemplifies well the general cranial condition in the python-like snakes; *Epicrates cenchris* is likewise a "typical" example of the boa-like snakes. Following the preceding descriptions of these forms, a comparison may now be made of

the two subgroups with reference to certain of the more salient cranial characteristics. The positive (+) sign denotes presence of the character, while the negative (—) sign denotes absence. Snakes which deviate from the more typical condition of their subgroup, i.e. show the condition of the alternate subgroup, are in parentheses.

| CHARACTERS | CONDITION IN PYTHONS | CONDITION IN BOAS |
|---|---|---|
| Premaxillary teeth. | + *(Aspidites, Calabaria)* | — |
| Premaxilla with ascending process. | — | + *(Eryx, Lichanura)* |
| Septomaxilla bearing lateral process. | + *(Loxocemus)* | — |
| Horizontal portions of vomers distinct from vertical parts caudally. | — *(Aspidites, Calabaria, Loxocemus)* | + *(Acrantophis, Corallus, Candoia carinata, Sanzinia)* |
| Only the upper portions of the frontals involved in naso-frontal articulation. | + *(Chondropython)* | — *(Candoia bibroni, C. carinata, Ungaliophis)* |
| Supraorbital bones. | + | — |
| Postorbital bones bilobed dorsally. | + *(Calabaria, Loxocemus)* | — |
| Inner maxillary process "swept" backward. | — *(Python anchietae, P. regius, Calabaria)* | + *(Charina, Epicrates gracilis)* |
| Lachrymal foramen completely enclosed by the prefrontal. | + (one of two specimens of *Calabaria*) | — *(Corallus caninus)* |
| Foramen of the palatine completely enclosed by that bone. | + *(Calabaria, Liasis amethystinus)* | — |
| Palatine continued backward as a spine. | + *(Liasis amethystinus)* | — *(Charina, Lichanura, Ungaliophis)* |
| Quadrate length less than ¼ of the distance from premaxilla to occipital condyle. | + *(Aspidites, Morelia, Chondropython, Liasis amethystinus)* | — *(Eryx johni, Candoia bibroni)* |

| CHARACTERS | CONDITION IN PYTHONS | CONDITION IN BOAS |
|---|---|---|
| Longitudinal distance from basipterygoid processes to level of quadrate-pterygoid joint nearly as great as ½ (more than 40%) of total skull length. | — *(Chondropython, Morelia, Liasis amethystinus, Python anchietae, P. regius)* | + *(Charina, Eryx johni, Epicrates gracilis, Ungaliophis)* |

## ABBREVIATIONS USED IN TEXT FIGURES

*al*, anterior lobe of postorbital; *an*, angular; *bo*, basioccipital; *bs*, basisphenoid; *co*, coronoid; *de*, dentary; *ec*, ectopterygoid; *eo*, exoccipital; *fr*, frontal; *lp*, lateral process of septomaxilla; *max*, maxilla; *na*, nasal; *opc*, opening for premaxillary channels; *pa*, parietal; *pal*, palatine; *pas*, ascending process of premaxilla; *pf*, prefrontal; *pl*, posterior lobe of postorbital; *pm*, premaxilla; *pmt*, premaxillary tooth; *pn*, processus nasalis; *po*, postorbital; *pp*, processus palatini; *pr*, prootic; *pra*, prearticular process; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *s*, stapes; *sm*, septomaxilla; *so*, supraorbital; *soc*, supraoccipital; *sp*, splenial; *st*, supratemporal; *sur*, surangular process; *tf*, tooth fossa; *vo*, vomer; *x*, horizontal frontal suture.

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# THE GENUS TETRAGNATHA (ARANEAE, ARGIOPIDAE) IN MICHIGAN

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No. 9 — *The Genus Tetragnatha (Araneae, Argiopidae) in Michigan*

By Arthur M. Chickering

I have recently completed studies on the genus *Tetragnatha* Latreille, 1804, in Central America and the West Indies (1957). It was only natural, therefore, for me to turn my attention to the genus as it is known in Michigan. The present paper is an outgrowth of that decision and with it I return once more to the study of my collections of Michigan spiders which have been accumulating for thirty years. The paper is offered with the hope that it will be of some help to those who are in the process of becoming acquainted with this highly interesting segment of our local fauna.

## Genus Tetragnatha Latreille, 1804

(Long-jawed orbweavers)

As Seeley (1928) has shown, *Eugnatha* and *Eucta* are synonyms of *Tetragnatha*. This genus, as now understood, may be defined as follows: The body is long and slender, usually several times as long as wide. The legs are long, slender, and usually spiny but there are notable exceptions, as in *T. tenuissima* O. P. Cambridge, widely distributed in Mexico, Central America, West Indies, and northern South America. When at rest, the two anterior pairs of legs are extended forward and the remaining two pairs are directed backward. In general, the carapace is somewhat oval, widest near the middle, flattened, and has a conspicuous median pit rather than a typical longitudinal groove. The eight eyes are in two rows which may be parallel, divergent, or convergent, but the lateral eyes are never contiguous. The chelicerae are usually very strongly developed, especially in males. There are numerous teeth along the fang groove on both margins and they are of considerable importance in the identification of species. However, the teeth are subject to differences in relative size, number, and relative position. Males always have a prolateral spur on the basal segment of the

chelicerae and this is also frequently of importance in determining species. The maxillae are essentially parallel, long, and dilated distally. The genital furrow is procurved and its shape can be used to some extent in distinguishing females, always more difficult to identify than are the males. A definite epigynum is entirely lacking in females. The spinnerets are terminal except in a few species in which the abdomen is considerably extended posteriorly.

Male palp: The cymbium is a narrow flap extending the whole length of the bulb. The paracymbium, attached to the base of the cymbium, often has a rather characteristic form peculiar to certain species. The conductor, in close association with the embolus, usually terminates in a characteristic form of specific value. All mature males which I have seen have a more or less conspicuous pit near the distal end of the cymbium suggestive of a sense organ.

The majority of the species in this genus appear to prefer to build their webs in grass and among the weeds in meadows close to water. I have collected large numbers among sedges and other plants over water in Panama and Jamaica. The webs are usually inclined but sometimes horizontal, with the spider at the open hub.

### *Key to the Species of* Tetragnatha *in Michigan*

#### Males

1. Lateral eyes clearly further from one another than AME are from PME (*caudata, pallescens, straminea, vermiformis*) ..... 2
1. Lateral eyes not clearly further from one another than AME are from PME; either definitely closer together than AME are to PME or about the same distance apart (*elongata, guatemalensis, harrodi, laboriosa, rusticana, versicolor*) ..... 5
2. Palpal tibia much longer than palpal patella (*pallescens, straminea*) .. 3
2. Palpal tibia and palpal patella about the same length (*caudata, vermiformis*) ..... 4
3. Basal segment of chelicera nearly as long as the cephalothorax; prolateral spur not definitely bifid but with a small tooth below apex ..... *pallescens*, p. 487
3. Basal segment of chelicera only a little more than half as long as the cephalothorax and definitely concave along outer border; prolateral spur clearly bifid at apex ..... *straminea*, p. 494

4. Abdomen definitely continued into a distinct "tail" posterior to spinnerets ..... *caudata*, p. 479
4. Abdomen not notably continued posterior to spinnerets ..... *vermiformis*, p. 495
5. Promargin of fang groove with a very large tooth near the middle of the row of promarginal teeth (*elongata, laboriosa, rusticana, versicolor*) ..... 6
5. Promargin of fang groove without a very large tooth near the middle of the row of promarginal teeth (*guatemalensis, harrodi*) ..... 9
6. Conductor of palp somewhat club-shaped distally, bluntly rounded and with a more or less conspicuous oval concavity near distal end ..... *versicolor*, p. 497
6. Conductor of palp not club-shaped distally and without any conspicuous oval concavity near distal end ..... 7
7. Palpal tibia much elongated; twice as long as palpal patella ..... *elongata*, p. 480
7. Palpal tibia not so notably elongated; less than twice as long as palpal patella ..... 8
8. Palpal conductor terminating in a beak-like structure; palpal tibia only slightly longer than palpal patella ..... *laboriosa*, p. 486
8. Palpal conductor terminating in a complicated hooked structure with a small rounded concavity behind the hooks; palpal tibia considerably longer than palpal patella ..... *rusticana*, p. 489
9. Paracymbium of male palp terminating in a long, slender, digital extension ..... *guatemalensis*, p. 482
9. Paracymbium terminating in a bluntly rounded distal end, not extended into a slender digital structure ..... *harrodi*, p. 484

## Females

1. Lateral eyes clearly further from one another than AME are from PME (*caudata, pallescens, straminea, vermiformis*) ..... 2
1. Lateral eyes not clearly further from one another than AME are from PME; either definitely closer together than AME are to PME or about the same distance apart (*elongata, guatemalensis, harrodi, laboriosa, rusticana, versicolor*) ..... 5
2. Abdomen considerably extended into a "tail" posterior to spinnerets ..... *caudata*, p. 479
2. Abdomen at most only extended a short distance posterior to spinnerets (*pallescens, straminea, vermiformis*) ..... 3
3. With a small dorsal tubercular tooth on fang near base; with a blunt tubercular tooth on basal segment of chelicera near base of fang ..... *straminea*, p. 494

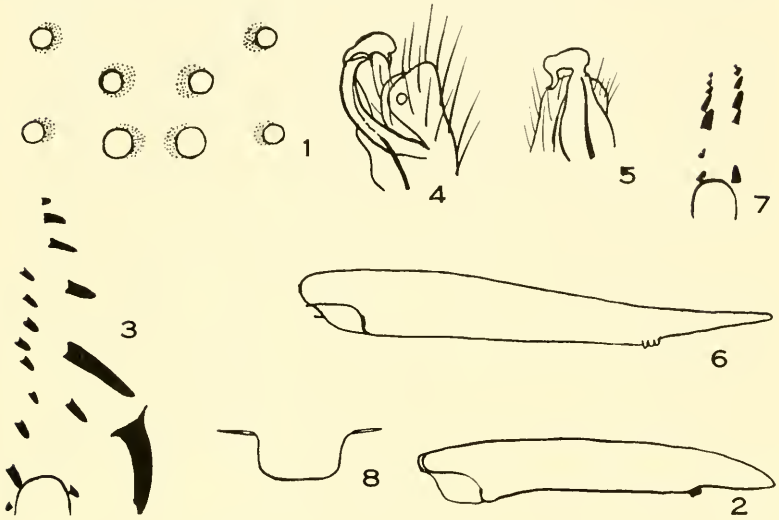
3. Without any dorsal tooth on fang near base; without any dorsal tooth on basal segment of chelicera near base of fang (*pallescens, vermiformis*) ..... 4
4. Fang distinctly sinuate; a wide space between small teeth along margins of fang groove near base of fang and those more remote; chelicerae extending forward in a nearly horizontal position, nearly as long as cephalothorax ..... *pallescens*, p. 487
4. Fang not distinctly sinuate; space between small teeth near base of fang and those more remote along fang groove not unusually great; chelicerae less horizontal in position, not more than half as long as cephalothorax ..... *vermiformis*, p. 495
5. Basal segment of chelicera nearly as long as cephalothorax; with a dorsal tooth on basal segment of chelicera near base of fang.. *elongata*, p. 480
5. Basal segment of chelicera considerably shorter than cephalothorax; without any dorsal tooth on basal segment of chelicera near base of fang (*guatemalensis, harrodi, laboriosa, rusticana, versicolor*) ....6
6. Abdomen conspicuously silvery on dorsal and dorsolateral sides; venter with a median dark stripe and a narrower silvery stripe on each side; lateral eyes as far apart as AME are from PME..... *laboriosa*, p. 486
6. Abdomen not conspicuously silvery on dorsal and dorsolateral sides; venter less distinctly striped; lateral eyes closer to one another than AME are to PME (*guatemalensis, harrodi, rusticana, versicolor*) ...7
7. Promargin of fang groove with a relatively large tooth between two small teeth near base of fang together with four relatively large teeth following a long toothless space (Fig. 39)..... *rusticana*, p. 489
7. Promargin of fang groove with teeth not arranged as stated above (*guatemalensis, harrodi, versicolor*) ..... 8
8. Promargin of fang groove with about nine teeth and with a very long toothless space between second and third teeth; retromargin with about eight teeth ..... *versicolor*, p. 497
8. Promargin of fang groove with about five or six teeth and with no very long toothless space (*guatemalensis, harrodi*) ..... 9
9. Both margins of fang groove with five teeth..... *harrodi*, p. 484
9. Both margins of fang groove with more than five teeth ..... *guatemalensis*, p. 482

N. B. The part of the key dealing with males, given in the preceding pages, should prove quite workable. It is a very difficult matter, however, to provide clearly workable keys for the identification of females because of the close similarities among the species and puzzling variations within each species. It is my opinion that these facts have not usually been sufficiently appreciated by those who have dealt with the taxonomy of this genus.

## Tetragnatha caudata Emerton, 1884

(Figures 1-8)

*Eucta lacerta* Petrunkevitch, 1911
*T. caudata* Seeley, 1928
*T. lacerta* Roewer, 1942
*T. caudata* Kaston, 1948
*T. caudata* Levi, 1954




External Anatomy of *T. caudata*
(Figures 1-8)

Fig. 1. Eye group of male seen from in front.
Fig. 2. Outline of male abdomen to show "tail"; lateral view.
Fig. 3. Left male cheliceral teeth; ventrolateral view.
Figs. 4-5. Two different views of tip of left male palp to show form of conductor.
Fig. 6. Outline of female abdomen to show "tail"; lateral view.
Fig. 7. Left female cheliceral teeth; from below.
Fig. 8. Form of genital groove.

*Male hypotype.* Total length 8.80 mm., exclusive of the chelicerae whose basal segment is a little more than one half as long as the cephalothorax. The whole body is long and slender with

the abdomen extending posterior to the spinnerets to form a distinct "tail" (Fig. 2). The abdomen is notched at the base above. The lateral eyes are nearly twice as far from one another as AME are from PME (Fig. 1). Chelicerae: promargin of fang groove with seven teeth and retromargin with nine; the prolateral spur is not definitely bifid but it has a small tubercle beneath the apex (Fig. 3). Leg spines are few and fragile. Palp: both tibia and patella are short; exclusive of the distal chitinous extension on the tibia, the two segments are nearly equal in length; the termination of the conductor is best shown in Figures 4 and 5. Color: cephalothorax with a pair of dark dorsal parallel stripes; the sternum is broadly dark along the margins with a lighter central portion; abdomen with a moderately broad yellowish-brown ventral stripe; laterally and dorsally the abdomen has many light golden spangles.

*Female hypotype.* Total length, exclusive of the chelicerae 13 mm. The whole body is long and slender with the "tail" extending behind the spinnerets for more than one fifth the total length of the body (Fig. 6). Chelicerae: basal segment about half as long as cephalothorax, moderately robust; the promargin of the fang groove has six teeth and the retromargin has seven (Fig. 7); base of the fang with a low blunt cusp on the dorsal side; fang slightly sinuous. The abdomen is notched at the base above. The color is essentially like that of the male. The form of the genital groove is shown in Figure 8.

As in many other species in this genus, I have noted a rather disconcerting variation in the number and placement of the chelicieral teeth in both sexes of *T. caudata.*

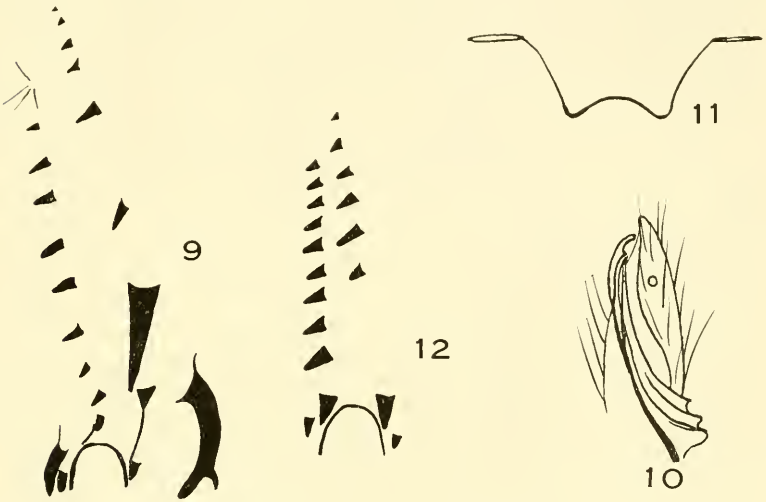
*Collection records:* The hypotypes are from Concord, Jackson Co., May 24, 1942. Other records are: Branch Co., Calhoun Co., Cheboygan Co., Emmet Co., Livingston Co., and Mecosta Co.

### Tetragnatha elongata Walckenaer, 1805

(Figures 9-12)

*T. grallator* Emerton, 1884
*T. elongata* Seeley, 1928
*T. elongata* Comstock, 1940
*T. elongata* Kaston, 1948
*T. elongata* Levi, 1954

*Male hypotype.* Total length, exclusive of the chelicerae, 8.32 mm. Chelicerae: basal segment somewhat longer than cephalothorax; the prolateral spur is strongly bifid; promargin of fang groove with nine teeth and retromargin with eleven, and both rows with teeth irregularly placed; fang undulates from base to apex (considerable variation in numbers of teeth and their




External Anatomy of *T. elongata*
(Figures 9-12)

Fig. 9. Left cheliceral teeth of male from below.
Fig. 10. Tip of male palp to show apex of conductor and related parts.
Fig. 11. Form of genital groove of female.
Fig. 12. Left cheliceral teeth of female from below.

placement has been noted among numerous specimens) (Fig. 9). Lateral eyes much closer to one another than AME are to PME. Legs with many moderately long, slender spines. The abdomen is not notched at its base above. Palp: Tibia nearly twice as long as patella; cymbium rounded distally; conductor terminates as shown in Figure 10.

*Female hypotype.* Total length, exclusive of the chelicerae, 9 mm. Abdomen considerably swollen in anterior half. Chelicerae: about five-sevenths as long as cephalothorax; the fang is very sinuous and has a large dorsal basal tooth; the basal segment also has a small dorsal distal tooth (Fig. 12). The base of the abdomen is concave but is not notched. The form of the genital groove is shown in Figure 11.

*Collection records.* The hypotypes are from Conway, Emmet Co., August, 1937. Numerous specimens from both Upper and Lower Peninsulas. Seems to be fairly common.

### Tetragnatha guatemalensis O. P. Cambridge, 1889

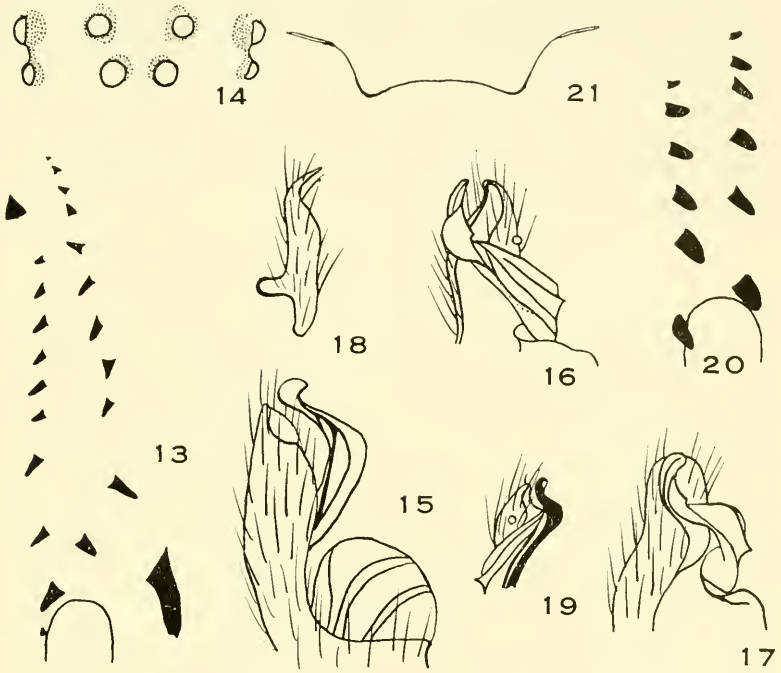
(Figures 13-21)

*T. seneca* Seeley, 1928
*T. banksi* Levi and Field, 1954
*T. guatemalensis* Roewer, 1942
*T. guatemalensis* Kraus, 1955
*T. guatemalensis* Chickering, 1957

In connection with my study of the genus *Tetragnatha* in Jamaica and other nearby islands (1957), I have already pointed out that I was compelled to consider *T. senoca* Seeley as a synonym for *T. guatemalensis* O. P. Cambridge. In connection with my study of the genus in Michigan I have again had this question under consideration and once more I have been driven to the same conclusion unlikely as it may seem. Drs. Levi and Field (1954) have apparently agreed that *T. seneca* Seeley is the same as *T. banksi* McCook, 1893.

*Male hypotype.* Total length, exclusive of the chelicerae, 7.8 mm. Chelicerae: basal segment about as long as the cephalothorax; there are eleven teeth along the promargin of the fang groove and ten along the retromargin but variations in number have been noted among numerous specimens; the prolateral spur is not clearly bifid but is bevelled distally (Fig. 13). Eyes: viewed from above, both rows recurved; central ocular quadrangle considerably wider behind than in front; lateral eyes much closer to one another than AME are to PME; ratio of eyes AME : ALE : PME : PLE = 12 : 9 : 10 : 10; lateral eyes separated from one another by slightly more than the diameter

of PLE (Fig. 14). Color quite dark and folium rather indistinct. Palp: tibia longer than patella in ratio of about 40 : 23, but both are of moderate length; the paracymbium terminates in a




External Anatomy of *T. guatemalensis*
(Figures 13-21)

Fig. 13. Left male cheliceral teeth from below.
Fig. 14. Eyes of male from in front.
Figs. 15-17. Distal end of left male palpal tarsus in different views.
Fig. 18. Paracymbium of male to show characteristic termination.
Fig. 19. Apex of right male palpal tarsus.
Fig. 20. Left female cheliceral teeth from below.
Fig. 21. Form of genital groove of female.

slender digital extension, apparently found in no other species in North or Central America (Fig. 18); the conductor terminates in a very characteristic form (Figs. 15-17, 19).

*Female hypotype.* Total length, exclusive of the chelicerae, 7.475 mm. Chelicerae: basal segment a little more than one-half the length of the cephalothorax; both margins of the fang groove with six teeth (Fig. 20); the fang has a very small basal dorsal cusp; the inner margin of the fang is irregular but without teeth. The form of the genital area is shown in Figure 21 (somewhat distorted in hypotype because of shrinkage of the specimen).

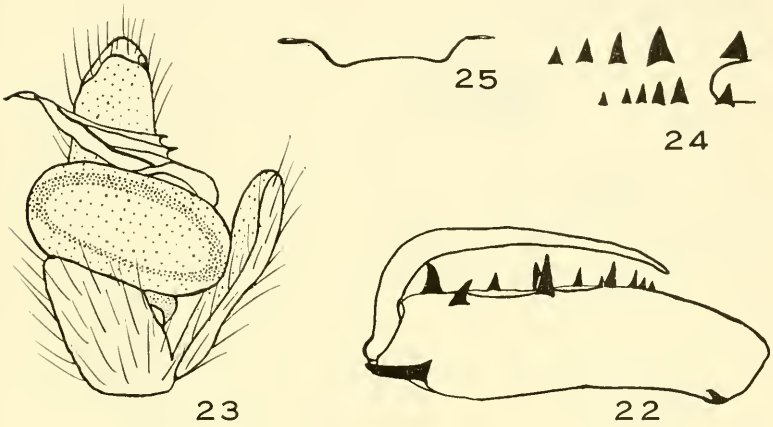
*Collection records.* The male and female hypotypes are from Emmet County, July and August, 1938 and 1937, respectively. Other specimens in my collection are from Emmet, Cheboygan, Mecosta, and Calhoun Counties.

### Tetragnatha harrodi Levi, 1951

(Figures 22-25)

*Male hypotype.* Total length, exclusive of the chelicerae 6.175 mm. Chelicerae: basal segment 1.755 mm. long; about two-thirds as long as the cephalothorax; the promargin of the fang groove has six teeth, the last three of which are small and close together; the retromargin has six teeth, the last two of which are small and close together; the prolateral spur is rather blunt at the apex and without any definite bifidity (Fig. 22). The lateral eyes are only a little more than two-thirds as far from one another as AME are from PME. Ratio of eyes AME : ALE : PME : PLE = 9.5 : 8 : 10 : 8. Central ocular quadrangle wider behind than in front in ratio of about 9 : 7. Width of clypeus equal to a little more than 1.5 times the diameter of AME. Base of abdomen somewhat swollen. Color: carapace reddish brown without distinct markings; sternum yellowish without distinct markings; legs, chelicerae, and palps light reddish brown; abdomen light with many small silvery flecks on dorsum, with narrow broken black lines alternating with narrow broken light lines along lateral sides, and with venter light with fine silvery flecks. Palp: tibia and patella short with tibia longer than patella in ratio of about 4 : 3; the paracymbium is blunt apically; the conductor terminates in a slender, somewhat twisted spine; the bulb is broad and short (Fig. 23).

*Female hypotype.* Total length, exclusive of the chelicerae, 5.20 mm. Color: essentially as in male but there are black dorsolateral spots and stripes of variable size and shape. The chelicerae are about one-third as long as the cephalothorax; the cheliceral teeth are as represented in Figure 24. The abdomen is somewhat swollen about one-third back from base. The genital




External Anatomy of *T. harrodi*
(Figures 22-25)

Fig. 22. Prolateral view of left chelicera with teeth.
Fig. 23. Distal end of left male palp; lateral view.
Fig. 24. Left female cheliceral teeth.
Fig. 25. Form of the genital groove of female.

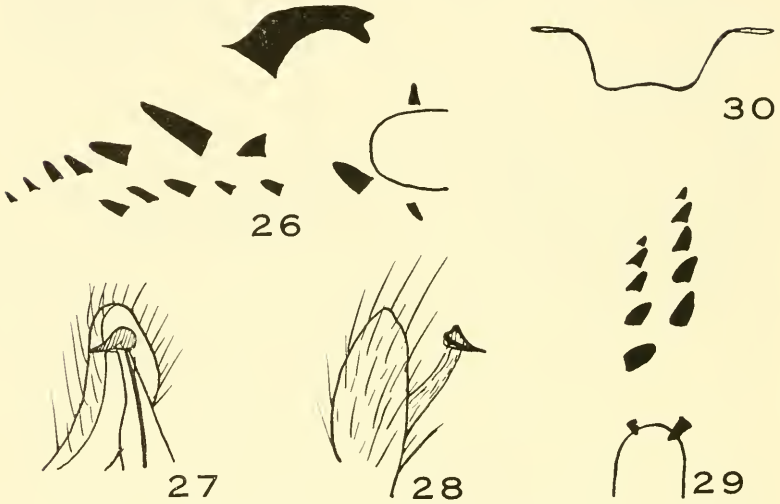
groove is essentially as represented in Figure 25. The specimen is probably not mature and, hence, some of its most important features may not be evident.

*Collection records.* The hypotypes are from Bay View, Emmet Co., August, 1941. No other specimens have yet appeared in my collection.

## Tetragnatha laboriosa Hentz, 1850

(Figures 26-30)

*T. illinoisensis* Keyserling, 1879
*T. alba* F. P. Cambridge, 1903
*T. alba* Petrunkevitch, 1911
*T. laboriosa* Petrunkevitch, 1911
*T. laboriosa* Kaston, 1948
*T. laboriosa* Levi, 1954




External Anatomy of *T. laboriosa*
(Figures 26-30)

Fig. 26. Left chelicoral teeth of male.
Figs. 27, 28. Two different views of the apex of the male cymbium and conductor.
Fig. 29. Left female chelicoral teeth.
Fig. 30. Form of female genital groove.

I have already indicated in a previous paper that I first became aware that *T. alba* F. P. Cambridge is a synonym of *T. laboriosa* Hentz when Dr. W. J. Gertsch suggested this in notes on certain species of the genus from Panama.

*Male hypotype.* Total length, exclusive of chelicerae, 5.07 mm. Chelicerae: basal segment about four-sevenths as long as cephalothorax; the prolateral spur is bifid; the promargin of the fang groove has about eight teeth including the "large tooth"; the retromargin has about seven (differences between numbers on right and left sides have been noted); the fang is slightly bent (Fig. 26). The lateral eyes are about as far apart as AME are from PME. Legs with numerous short slender spines. Palp: tibia a little longer than patella but both are short (ratio about 7 : 5); conductor as shown in Figures 27 and 28.

*Female hypotype.* Total length, exclusive of the chelicerae, 5.75 mm. Chelicerae: basal segment about half as long as cephalothorax; relatively robust; promargin of fang groove with six teeth; retromargin with six but the two sides are not in full agreement (Fig. 29); considerable variation has been noted in respect to numbers of cheliceral teeth in different specimens. Color: with a well defined folium; conspicuously silvery on dorsal and dorsolateral sides; there is a midventral dark brown or black stripe with a silvery stripe on each side of it. The form of the genital groove is shown in Figure 30.

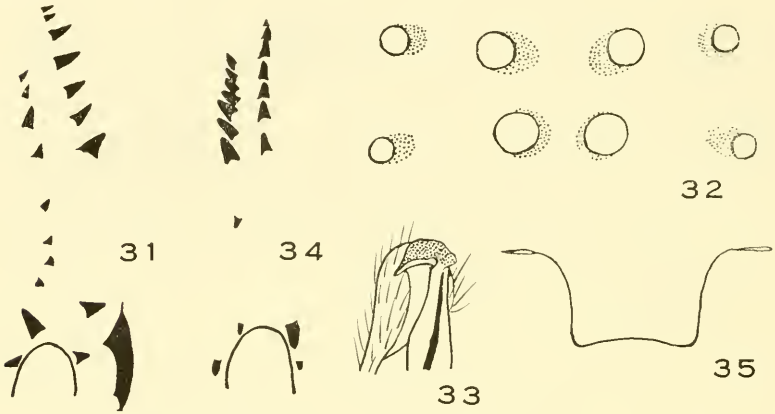
*Collection records.* This seems to be our commonest species. It is in my collection from many parts of the state, both Upper and Lower Peninsulas. The species is often found in large numbers in webs built among grass tops at some distance from water. Seeley (1928) reported it as being abundant in an oat field just before the grain was cut.

### Tetragnatha pallescens F. P. Cambridge, 1903

(Figures 31-35)

*T. pallida* Banks, 1892
*T. pallescens* F. P. Cambridge (*pallida* preoccupied by O. P. Cambridge, 1889)
*Eugnatha pallescens* Petrunkevitch, 1911
*T. pallescens* Seeley, 1928
*T. pallescens* Comstock, 1940
*T. pallescens* Kaston, 1948
*T. pallescens* Levi, 1954

*Male hypotype.* Total length, exclusive of the chelicerae, 8 mm. Chelicerae; basal segment about as long as cephalothorax; teeth along fang groove as shown in Figure 31 (minor differences noted between right and left sides); prolateral spur not distinctly bifid but there is a small tooth below the apex; the fang is slightly sinuate; there is no "large tooth" on the promargin. The lateral eyes are further from one another than AME are from PME in ratio of about 26 : 15 (Fig. 32). Palp: tibia longer than




External Anatomy of *T. pallescens*
(Figures 31-35)

Fig. 31. Left male cheliceral teeth from below.
Fig. 32. Eye-group of male from in front.
Fig. 33. Tip of conductor of male palp.
Fig. 34. Left female cheliceral teeth from below.
Fig. 35. Form of the genital groove in the female.

patella in ratio of about 9 : 5; the conductor has a very characteristic, somewhat sickle-shaped apex (Fig. 33). The base of the abdomen is notched.

*Female hypotype.* Total length, exclusive of the chelicerae, 10.40 mm. Chelicerae: basal segment about four-fifths as long as cephalothorax; extend forward nearly horizontal; promargin of fang groove with nine teeth and retromargin with ten (Fig. 34); with no more than tips of fangs covered by maxillae when

the former are folded; fang only slightly sinuate and without any dorsal basal cusp. The eyes are like those of male. Abdomen: gently notched at base; long and slender; somewhat swollen in anterior third; very slightly extended posterior to spinnerets. Color: the carapace has a faint median dark stripe constricted at the median thoracic pit and also a faint marginal stripe; the dorsum has many small silvery spangles much less conspicuous than in *T. laboriosa;* the lateral abdominal sides have many of these spangles and irregular brownish spots; the venter has a faint brownish median stripe. The genital groove is as shown in Figure 35.

*Collection records.* Seems to be fairly common in Michigan; usually taken in marsh grass and around bodies of water. Emerton observed them mating in early September. The species is in my collection from numerous localities in the Lower Peninsula.

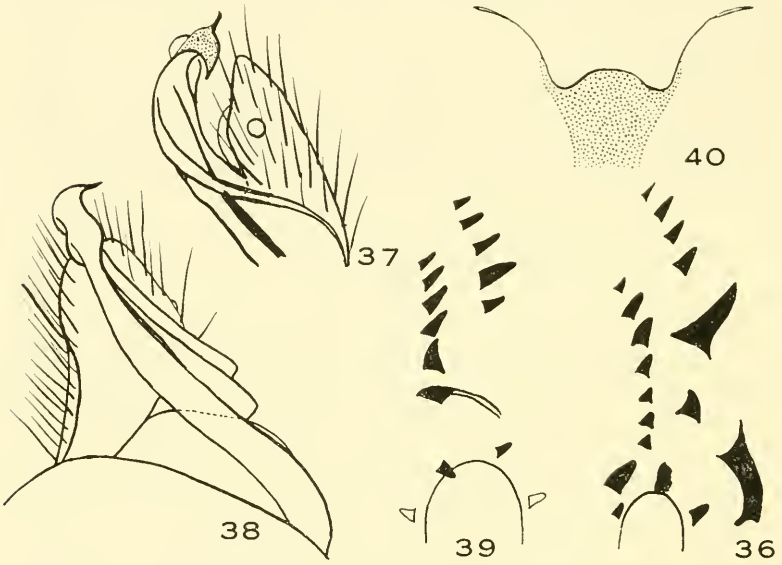
### Tetragnatha rusticana sp. nov.

(Figures 36-40)

*Male holotype.* Total length, exclusive of the chelicerae, 6.7 mm.; including chelicerae 8.0 mm. long. Carapace 2.60 mm. long, 1.56 mm. wide opposite second coxae where it is widest; with the usual form and with the median depression which is a pit rather than a groove and somewhat wider than long.

*Eyes.* Eight in two rows as usual; ocular tubercles moderately developed; viewed from above, both rows moderately recurved: viewed from in front, anterior row nearly straight and posterior row slightly procurved, both measured by centers. Central ocular quadrangle wider behind than in front in ratio of about 4 : 3. Ratio of eyes AME : ALE : PME : PLE = 8 : 5.5 : 9 : 7. AME separated from one another by about five-fourths of their diameter, from ALE by about nine-fourths of their diameter. PME separated from one another by nearly twice their diameter, from PLE by slightly more than twice their diameter. Laterals separated from one another by about 1.5 times the diameter of AME. AME separated from PME by a little less than twice their diameter, hence further apart than ALE are from PLE.

*Chelicerae.* Well developed; moderately porrect; quite divergent in distal two-thirds; considerably swollen in distal half; quite concave along outer border; a little less than two-thirds as long as cephalothorax; fang is long, slender, and only slightly sinuate; prolateral spur definitely bifid with lower division the more robust; the promargin of the fang groove has the "large tooth" together with six others; the retromargin has a total of nine teeth all spaced essentially as shown in Figure 36.




External Anatomy of *T. rusticana* sp. nov.
(Figures 36-40)

Fig. 36. Left male cheliceral teeth from below.

Figs. 37, 38. Two different views of the apex of the male palpal tarsus to show distinctive features of the conductor.

Fig. 39. Left female cheliceral teeth from below.

Fig. 40. Form of the female genital groove.

*Maxillae.* Nearly parallel; moderately broadened distally; with ridge and groove extending somewhat obliquely along posterior surface; longer than lip in ratio of about 7 : 3; more than four times as long as wide in middle.

*Lip.* Wider at base than long in ratio of about 4 : 3; strongly chitinized and rough except at distal border which is conspicuously separated from remainder; sternal suture gently procurved; sternal tubercles at ends of sternal suture short and bluntly pointed.

*Sternum.* Convex; narrowly scutiform; longer than wide in ratio of 4 : 3; continued by a narrow sclerite between fourth coxae which are separated by a little less than one-third of their width.

*Legs.* 1423. Width of first patella at "knee" .264 mm., tibial index of first leg 4. Width of fourth patella at "knee" .242 mm., tibial index of fourth leg 5.

| | Femora | Patellae | Tibiae | Metatarsi | Tarsi | Totals |
|---|---|---|---|---|---|---|
| | (All measurements in millimeters) | | | | | |
| 1. | 5.785 | 1.040 | 6.175 | 6.500 | 1.625 | 21.125 |
| 2. | 4.160 | .890 | 3.185 | 4.275 | .975 | 13.435 |
| 3. | 2.360 | .460 | 1.430 | 1.820 | .650 | 6.720 |
| 4. | 4.680 | .845 | 4.030 | 4.420 | .910 | 14.885 |
| Palp | 1.690 | .455 | .660 | —— | .975 | 3.780 |

Numerous moderately long and slender spines together with a moderately well-developed coat of hair are present on all legs. It is difficult to distinguish, without special study, the long and slender erect hairs particularly numerous on the posterior legs from true trichobothria.

*Palp.* The tibia is longer than patella in about the ratio of 3 : 2 but both are of moderate length; both cymbium and paracymbium are of usual shape without especially distinctive features. The distinctive features of the conductor are probably best shown in Figures 37, 38.

*Abdomen.* 4.355 mm. long; slender and not swollen in any region; extends a short distance posterior to spinnerets; unnotched at base.

*Color in alcohol.* Carapace, legs, and nearly all mouth parts appear to be of varying shades of yellowish brown. The lip is brown with distal yellowish border. The sternum is colored more deeply around its periphery but is also yellowish brown in general. Abdomen: dorsally and dorsolaterally there are many

golden spangles with a faintly outlined iridescent striping with a reddish tinge along lateral sides; the venter is also moderately well covered by golden spangles with just a suggestion of a brown median stripe which is prominent in the female.

*Female allotype.* Total length, exclusive of the chelicerae, 8.125 mm.; including chelicerae the length is 8.45. Carapace 2.5 mm. long, 1.625 mm. wide opposite second coxae where it is widest; median thoracic depression very shallow.

*Eyes.* Ratio of eyes AME : ALE : PME : PLE = 10 : 6 : 8.5 : 6.5. AME separated from one another by nine-tenths of their diameter, from ALE by a little more than twice their diameter. PME separated from one another and from PLE by a little more than twice their diameter. ALE separated from PLE by a little less than twice the diameter of PLE; AME separated from PME by a slightly greater distance. Height of clypeus equal to about 1.5 times the diameter of AME.

*Chelicerae.* Well developed; only moderately porrect; quite divergent; outer border only slightly concave; fang groove with seven teeth along promargin and eight along retromargin, spaced as indicated in Figure 39. Fang slightly sinuate and bent rather sharply about the middle; with a low blunt basal dorsal cusp.

*Maxillae.* Nearly parallel; moderately broadened distally; covering tips of fangs when the latter are folded; somewhat concave along outer borders; about .88 mm. long; longer than lip in ratio of about 5 : 2; longer than wide in middle in ratio of about 8 : 3.

*Lip.* Wider at base than long in ratio of about 4 : 3; strongly chitinized and rough except at distal border; sternal suture plainly procurved and with the usual sternal tubercles at ends of suture.

*Sternum.* Convex; narrowly scutiform; longer than wide in ratio of 5 : 4; continued as a narrow sclerite between fourth coxae which are separated by a little less than one fourth of their width.

*Maxillae.* Nearly parallel; moderately broadened distally; covering tips of fangs when the latter are folded; somewhat concave along outer borders; about .88 mm. long; longer than lip in ratio of about 5 : 2; longer than wide in the middle in ratio of about 8 : 3.

*Lip.* Wider at base than long in ratio of about 4 : 3; strongly chitinized and rough at distal border; sternal suture plainly procurved and with usual sternal tubercles at ends of suture.

*Sternum.* Convex; narrowly scutiform; longer than wide in ratio of about 5 : 4; continued as a narrow sclerite between fourth coxae which are separated by a little less than one-fourth of their width.

*Legs.* 1243. Width of first patella at "knee" .308 mm., tibial index of first leg 5. Width of fourth patella at "knee" .220 mm., tibial index of fourth leg 7.

| | Femora | Patellae | Tibiae | Metatarsi | Tarsi | Totals |
|---|---|---|---|---|---|---|
| | (All measurements in millimeters) | | | | | |
| 1. | 4.875 | 1.170 | 5.005 | 5.395 | 1.235 | 17.680 |
| 2. | 3.575 | .912 | 2.925 | 3.347 | .910 | 11.669 |
| 3. | 1.755 | .520 | 1.170 | 1.430 | .552 | 5.427 |
| 4. | 3.780 | .650 | 2.600 | 3.250 | .715 | 10.995 |

Leg spines, hair, and trichobothria essentially as in male. Palpal claw as usual with a robust terminal tooth and a single row of slender teeth.

*Abdomen.* 6.175 mm. long; somewhat swollen in anterior half; extended somewhat posterior to spinnerets; acutely notched at base. The form of the genital groove is shown in Figure 40.

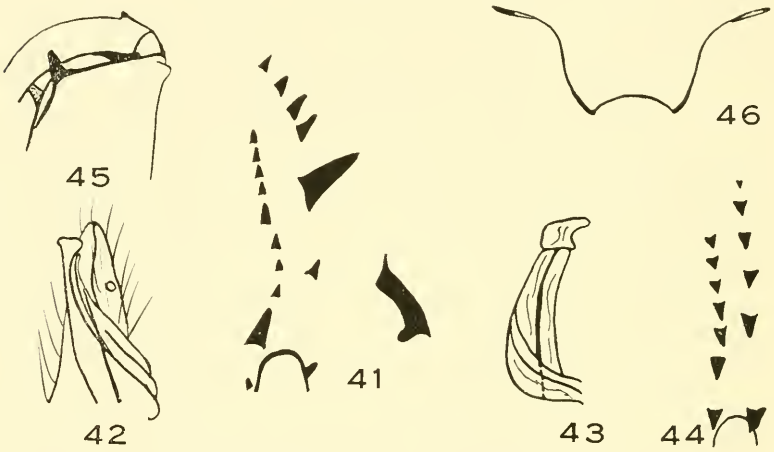
*Color in alcohol.* Carapace light yellowish-brown with a broad dusky stripe on each side diverging from the median pit to the lateral eyes. The sternum is brown with a median triangular spot reaching from the base of the lip for about there-fourths of the length of that part of the body. The lip is brown with a yellow border. The other mouth parts are varying shades of yellowish-brown. The legs are generally light yellowish-brown but the first femora are dusky gray beneath. Abdomen: the folium is well outlined and colored a rich reddish brown with small golden spangles; on each lateral side there is a dorsolateral silvery stripe and a ventrolateral brownish stripe with small golden spangles; the venter has a median dark brown stripe with a silvery stripe on each side of it; from the base of the anterior spinnerets a narrow dark brown stripe diverges to merge with the ventrolateral brown stripe.

*Type locality.* Both holotype and allotype are from Bay Co., Michigan, June, 1950, collected by R. R. Dreisbach. Paratypes of both sexes are in my collection from Aranac, Bay, Emmet, Huron and Washtenaw counties.

## Tetragnatha straminea Emerton, 1884

(Figures 41-46)

*Eugnatha straminae* Petrunkevitch, 1911
*T. straminea* Seeley, 1928
*T. straminea* Kaston, 1948
*T. straminea* Levi, 1954




External Anatomy of *T. straminea*
(Figures 41-46)

Fig. 41. Left male cheliceral teeth from below.
Fig. 42. Distal ends of conductor and cymbium.
Fig. 43. Distal end of conductor with cymbium removed; turned at right angles to Figure 42.
Fig. 44. Left female cheliceral teeth from below.
Fig. 45. Distal end of chelicera to show cusps at base of fang and basal segment of chelicera.
Fig. 46. Form of genital groove in female.

*Male hypotype.* Total length, exclusive of the chelicerae, 7.605 mm. Lateral eyes clearly further from each other than AME are

from PME. Slender throughout. Chelicerae: basal segment about half as long as cephalothorax; promargin with seven teeth including the "large tooth"; retromargin with ten teeth; the prolateral spur is distinctly bifid (Fig. 41); the fang is evenly curved. A little more than the tips of the fangs are hidden by the maxillae when the former are folded. Abdomen: shallowly notched at base; colored dorsally much like *T. laboriosa*; with a median ventral brownish stripe and a broad spangled stripe on each side. Palp: tibia twice as long as the patella; paracymbium curved and bluntly rounded distally; termination of conductor difficult to see but Figures 42 and 43 probably give a fairly accurate illustration of it.

*Female hypotype.* Total length, exclusive of the chelicerae, 8.45 mm. Eyes as in male. Abdomen plainly notched at base and slightly extended posterior to spinnerets. Maxillae hide a considerable portion of the fangs when the latter are folded. Chelicerae: fang with a small but distinct dorsal basal cusp; basal segment with a distinct blunt cusp near base of fang; promargin of fang groove with six teeth; retromargin with seven teeth (Figs. 44, 45). The form of the genital groove is shown in Figure 46. In collections this species frequently seems to have been confused with *T. laboriosa*.

*Collection records.* The hypotypes are from Albion, Calhoun Co., June, 1932. The species is in my collection from many localities in the Lower Peninsula and from Mackinac and Marquette counties in the Upper Peninsula.

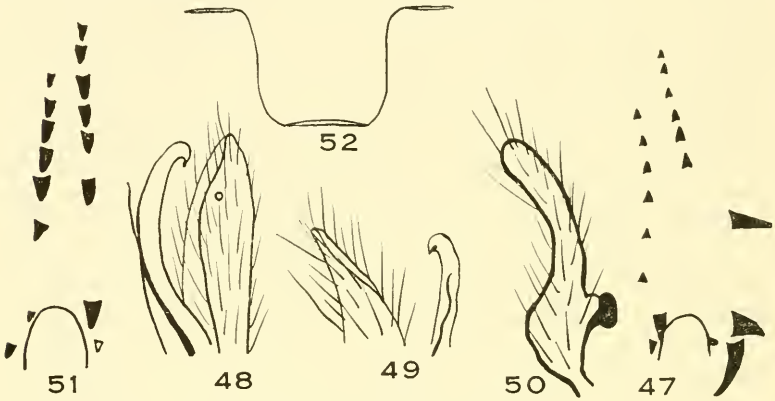
### Tetragnatha vermiformis Emerton, 1884

(Figures 47-52)

*Eucta vermiformis* Petrunkevitch, 1911
*T. vermiformis* Seeley, 1928
*T. vermiformis* Kaston, 1948
*T. vermiformis* Levi and Field, 1954
*T. vermiformis* Chickering, 1957

*Male hypotype.* Total length, exclusive of the chelicerae, 7.605 mm. Lateral eyes nearly twice as far from one another as AME are from PME. Chelicerae: basal segment about seven-ninths as long as the cephalothorax; the prolateral spur is not bifid; the fang is somewhat sinuate; the promargin of the fang groove has

nine teeth with two set far out of line; the retromargin has eight teeth (Fig. 47). Palp: both tibia and patella are short and nearly equal with tibia slightly the longer if the chitinous extension is included; the paracymbium is slender and gently curved in the distal half; the distal end of the conductor is characteristically hook-shaped (Figs. 48-50). The base of the abdomen is just slightly notched. The abdomen is silvery with gray reticulations and no folium dorsally.




External Anatomy of *T. vermiformis*
(Figures 47-52)

Fig. 47. Left male cheliceral teeth from below.

Figs. 48, 49. Two views of distal ends of cymbium, conductor, and embolus.

Fig. 50. Paracymbium of male.

Fig. 51. Left female cheliceral teeth from below.

Fig. 52. Form of the genital groove of female.

NOTE: Figs. 51, 52 are taken from Emerton's type specimen.

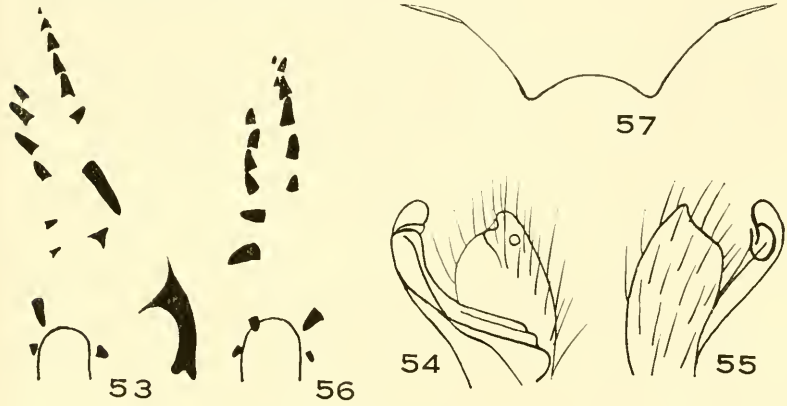
*Female hypotype.* Total length, exclusive of the chelicerae, 7.41 mm. Eyes essentially as in male. Chelicerae: basal segment less than one-half as long as cephalothorax; promargin of fang groove with eight teeth; retromargin also with eight teeth (Fig. 51); only tips of fang hidden by maxillae when the former are folded; fang slightly sinuate; outer border of basal segment only slightly concave. Genital groove essentially as shown in Figure 52.

*Collection records.* Levi and Field (1954) had only McCook's original "Wisconsin" record. The Michigan hypotypes are from Calhoun Co., Sept., 1933. Other specimens are in my collection from Bay, Branch, Calhoun, Emmet, Huron, and Mecosta counties. It appears to be uncommon; usually taken in marsh grass.

### Tetragnatha versicolor Walckenaer, 1841

(Figures 53-57)

*T. extensa* Emerton, 1884
*T. dentigera* F. P. Cambridge, 1903
*T. extensa* Petrunkevitch, 1911
*T. extensa* Seeley, 1928
*T. extensa* Comstock, 1940
*T. versicolor* Kaston, 1948
*T. versicolor* Levi and Field, 1954




External Anatomy of *T. versicolor*
(Figures 53-57)..

Fig. 53. Left male cheliceral teeth from below.
Fig. 54-55. Two views of the distal end of the cymbium and conductor of the male palp.
Fig. 56. Left female cheliceral teeth from below.
Fig. 57. Form of the genital groove in the female.

*Male hypotype.* Total length, exclusive of the chelicerae, 6.955 mm. Chelicerae: basal segment slightly more than four-

fifths as long as cephalothorax; prolateral spur clearly bifid; the promargin of the fang groove has nine teeth with the most proximal very small; the retromargin has eight (Fig. 53); the fang is not sinuate. Lateral eyes closer to one another than AME are to PME. Leg spines numerous, long, and slender. Palp: tibia longer than patella in ratio of 2 : 1; distinctive conductor shown in Figures 54 and 55. The base of the abdomen is not notched. The color and markings are highly variable but are, in general, similar to those of the female.

*Female hypotype.* Total length, exclusive of the chelicerae, about 9.425 mm. Abdomen clearly notched at base. Chelicerae: a little more than half as long as cephalothorax; fang only slightly sinuate; promargin of fang groove with nine teeth and the last three out of line; the retromargin has eight teeth (Fig. 56); a considerable amount of variation has been noted in the number of teeth along the fang groove in different specimens. The form of the genital groove is shown in Figure 57.

*Collection records.* The male hypotype is from Calhoun Co., May, 1942; the female hypotype is from Emmet Co., August, 1937. Other specimens are in my collection from many localities in the Lower Peninsula and from several localities in Marquette County in the Upper Peninsula.

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